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Seattle, Washington

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Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
Miami, FL 33149-1099

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LONGEVITY AND AGE VALIDATION OF A TAG-RECAPTURED ATLANTIC SAILFISH, *ISTIOPHORUS PLATYPTERUS*, USING DORSAL SPINES AND OTOLITHS

ERIC D. PRINCE,[1] DENNIS W. LEE,[1] CHARLES A. WILSON,[2]
AND JOHN M. DEAN[3]

ABSTRACT

A tagged female Atlantic sailfish, *Istiophorus platypterus*, of 24.6 kg (54 lb) was recaptured on 14 January 1984, after being at large for 10 yr and 10 mo (4,025 d). Approximate age based on tagging records ranged from at least 13 to 15+ yr. Maximum estimated longevity of this species was therefore revised upwards from previously reported ≥7 yr to at least 13-15+ yr. Estimates of age based on sections of dorsal spine numbers 3-6 ranged from 2 to 8 yr and substantially underestimated the range in age known from tagging records (13-15+ yr). This discrepancy was due to enlargement of the porous, vascularized core of spine sections which obscured zonations associated with early growth history. Thus, dorsal spines do not appear to be useful in ageing older sailfish (i.e., ≥5 yr). Age estimates from sagittae (otoliths) were 13 yr based on scanning electron microscope counts of external ridges and analysis of internal otolith microstructure. Otolith age, therefore, agreed with age known from tagging records. The relatively large size of the sagitta (7.84 mg) also provides additional evidence that the otolith could be from a very old sailfish. These data strongly suggest that in older, larger sailfish (≥5 yr, 22.7 kg), sagittae, rather than dorsal spines, should be used as the source of age and growth information.

The Atlantic sailfish, *Istiophorus platypterus*, is one of the most popular recreational fishes along the U.S. Atlantic coast, Gulf of Mexico, and Caribbean Sea. In fact, this species has been described as the most sought after fish by southeast marine charter boat anglers, particularly in south Florida (Ellis 1957). Although most landings of Atlantic sailfish in the southeastern United States are made by recreational anglers, many are also taken incidentally by domestic and foreign commercial longline vessels (Lopez et al. 1979). The biological information presently used in stock assessments of Atlantic sailfish (Conser 1984) consists of age and growth data derived exclusively from analysis of dorsal spines (Jolley 1974, 1977; Hedgepeth and Jolley 1983). However, uncertainties remain concerning Atlantic sailfish age structure, longevity, choice of skeletal structure for ageing, and rate of growth because of inconsistencies reported in the literature. In addition, the accuracy of age and growth estimates from skeletal structures and length-frequency analyses have not been validated for all age classes (de Sylva 1957; Jolley 1974, 1977; Radtke and Dean 1981; Hedgepeth and Jolley 1983).

One problem in using spines as a source of age and growth information is the tendency of the vascularized core to obscure zonations associated with early growth history. The enlargement of the vascularized core and subsequent reabsorption of tissues are most severe in the largest and oldest specimens (causing underestimates of true age) and have contributed to the lack of detailed information for older age classes. Several studies have also reported difficulty in interpreting the double and triple bands often observed in Atlantic sailfish spines (Jolley 1977; Hedgepeth and Jolley 1983). These problems are not unique to sailfish (Casselman 1983; Compean-Jimenez and Bard 1983) and have resulted in an unusually large proportion of spine samples (as much as 76%) being rejected for age and growth analysis (Jolley 1977). Radtke and Dean (1981) reviewed this problem and suggested that otoliths (sagittae) may be a better skeletal structure for age and growth assessment in sailfish because these structures do not have the disadvantages associated with the spinal core. For example, 98% of the otolith samples examined by Radtke and Dean (1981) were reportedly suitable for age and growth estimation. Even though these preliminary findings were

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[1] Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149-1099.

[2] Belle W. Baruch Institute for Marine Biology and Coastal Research, Department of Biology and Marine Science Program, University of South Carolina, Columbia, SC 29208; present address: Coastal Ecology and Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803-7503.

[3] Belle W. Baruch Institute for Marine Biology and Coastal Research, Department of Biology and Marine Science Program, University of South Carolina, Columbia, SC 29208.

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encouraging, use of otoliths to resolve age and growth discrepancies for Atlantic sailfish has not been reported, and no conclusive evidence is available to validate the accuracy of age estimates for this species using any method. We present an analysis of dorsal spines and otoliths obtained from one tag-recaptured Atlantic sailfish, where age was very closely approximated from tagging records, to help resolve the problems associated with ageing this species.

METHODS

The Cooperative Gamefish Tagging Program of the Southeast Fisheries Center Miami Laboratory recovered a tag from a female Atlantic sailfish, which had been recaptured on 14 January 1984, off Boynton Beach, FL (Prince and Lee 1984). This fish was originally tagged and released off the Florida Keys (Islamorada) on 5 March 1973, at an estimated weight of 18.2 kg (about 40 lb). When recaptured it weighed 24.6 kg (54 lb) and had a lower jaw fork length (LJFL) of 176.5 cm. The sailfish appeared to have a healthy external appearance when caught and body proportions and overall morphology were within the normal range for a specimen of this size. The entire fish was made available to us by J. T. Reese Taxidermist, Inc. (Ft. Lauderdale, FL), and both sagittae and the first six dorsal spines were sampled for age determination.

Dorsal Spine Analysis

Dorsal spines were collected from the tagged Atlantic sailfish following the procedures of Prince and Lee (1982). Past efforts to age sailfish using dorsal spines have relied on spine number 4 as the source of age and growth information (Jolley 1974, 1977; Hedgepeth and Jolley 1983). We collected the first six anterior dorsal spines to insure that the number assigned to each spine was accurate for identification and analysis and to gain information about possible differences between spines. The first two anterior dorsal spines of sailfish are greatly reduced in size compared with spines 3-6 and were not used to estimate age. In addition, spines posterior to spine number 6 have a smaller diameter and were not used for age determination. This decision was based, in part, on a report by Robins[4] and Robins and de Sylva (1963) who believed that the posterior dorsal spines of billfish do not grow throughout their entire lifetime and recommended that only anterior spines be used for age and growth studies.

Dorsal spines 3-6 were cleansed of tissue, labeled with a collection number, and preserved in isopropyl alcohol (98%). The methods of sectioning dorsal spines given by Hedgepeth and Jolley (1983) and Prince et al. (1984) were used in this study. Dorsal spine number 4 was sectioned by M. Y. Hedgepeth at the laboratory of the Florida Department of Natural Resources (FDNR), West Palm Beach, FL, to ensure that processing of this spine was identical with methods previously reported. We sectioned spines 3, 5, and 6 using a Buehler ISOMET[5] saw and a 10.16 cm diameter diamond wafer blade. At least 2 or 3 sections (0.44-0.46 mm thick) were taken from each spine. Additional sections were taken from spine number 4 after it had been processed by FDNR personnel. All spine sections were placed into labeled vials with isopropyl alcohol (98%) for storage and extraction of oil. A single section was selected and allowed to air dry before microscopic examination.

Dorsal spine sections were examined initially using a compound stereoscope (6.0×) with transmitted light in order to assess that portion of the section not affected by the vascularized core. Measurements (in millimeters, mm) of the solid bone area in the distal portion of the right lobe of each section were taken along a straight-line counting path from the focus to the outside margin of the structure.

We assigned an age to each spine by counting only concentric translucent bands that were continuous around the circumference of the entire section. In transmitted light, the zonations consisted of a dark opaque zone followed by a light translucent zone. D. W. Lee made three repeated counts of translucent zones using a compound stereoscope at 12.0 to 25.0× magnification.

Otolith Analysis

The general methods of Radtke and Dean (1981) and Wilson and Dean (1983) were used to extract and prepare the sagittae for examination by scanning electron microscopy (SEM) and light microscopy. The sagittae were removed from the tagged Atlantic sailfish, cleaned with sodium hypochloride solution, and rinsed in xylene and then 95% ethanol.

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[4] Robins, C. R., Professor, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, pers. commun. 1982.

[5] Reference to trade names and products does not imply endorsement by the National Marine Fisheries Service.

The weight of one air-dried otolith was measured to 0.001 mg (±5%) using a Perkin Elmer AD2Z ultra-microbalance. The sagitta was attached to an aluminum stub, coated with gold, and examined by SEM at 15.0-1500× to observe the surface morphology. External ridges on the rostral lobe of sailfish sagittae, first described by Radtke and Dean (1981), was one of the features used in this study for age estimation.

Following the methods of Haake et al. (1982) and Wilson and Dean (1983), the other member of the pair of sagittae was embedded in epoxy resin, and a section was made in the transverse plane by polishing both sides to 0.5 mm thickness with 600 grit sandpaper and 0.3 μm alumina polish. The internal structure of the sectioned sagitta was examined with an Olympus BH_2 compound microscope at 4.0 to 1200× to aid overall orientation and understanding of the growth of the structure and to interpret the external ridges used for age estimation.

RESULTS AND DISCUSSION

Our tagging records indicate that the tagged Atlantic sailfish recaptured on 14 January 1984, was at-large for 10 yr and 10 mo or 4,025 d. An experienced charter boat captain estimated its size when tagged to be 18.2 kg (40 lb). Bias in overestimating the size of billfish during tagging has been a common problem since the inception of the Cooperative Gamefish Tagging Program in 1954 (Prince 1984). However, we feel that such an error would probably not exceed ±4.6 kg (10 lb) in a fish of this size, particularly when the experience of the captain making the estimate is considered. The estimated age of a sailfish of about 18.2 kg (40 lb) would be 2-4 yr based on dorsal spine analysis (Jolley 1974, 1977; Hedgepeth and Jolley 1983) and 3-5 yr based on otolith analysis (Radtke and Dean 1981). Therefore, the approximate range in age of this sailfish based on tagging information is 13-15+ yr. We feel these are conservative figures based on the available information and it is highly unlikely that this fish could be younger than 13 yr.

Maximum longevity of Atlantic sailfish was first inferred by de Sylva (1957) to be at least 3 or 4 yr based on length-frequency analysis (Fig. 1). A modal group beyond 4 yr was indicated in his analysis but year class designation was not discussed. Since 1957, estimated longevity of Atlantic sailfish has been revised upwards (Fig. 1) to ≥7 yr. Our tagging records indicate, however, that the oldest Atlantic sailfish aged by dorsal spine analysis (Jolley 1977; estimated age 8) probably underestimates the maximum longevity of this species by a considerable margin. Although Jolley (1977) speculated that sailfish may live as long as 9 or 10 yr because the one age 8 individual was not the largest specimen in his sample, his estimated ages did not exceed 8 yr. In addition, the maximum estimated age reported in other recent studies was ≥7 yr (Radtke and Dean 1981; Hedgepeth and Jolley 1983). An Atlantic sailfish of estimated age 7 or 8 from the above sources corresponds to an average size of about 25 kg (55 lb). Since our records indicate the age of the tag-recaptured 24.6 kg (54 lb) sailfish was 13-15+ yr, it appears that maximum longevity of Atlantic sailfish could be considerably older, perhaps over 20 yr, because numerous specimens exceeding 45.5 kg (100 lb) have been caught during the last decade (Beardsley 1980). This reasoning assumes that sailfish have indeterminate growth throughout their entire lifetime and that their size is proportional to age. It also appears from tagging data that Atlantic sailfish may

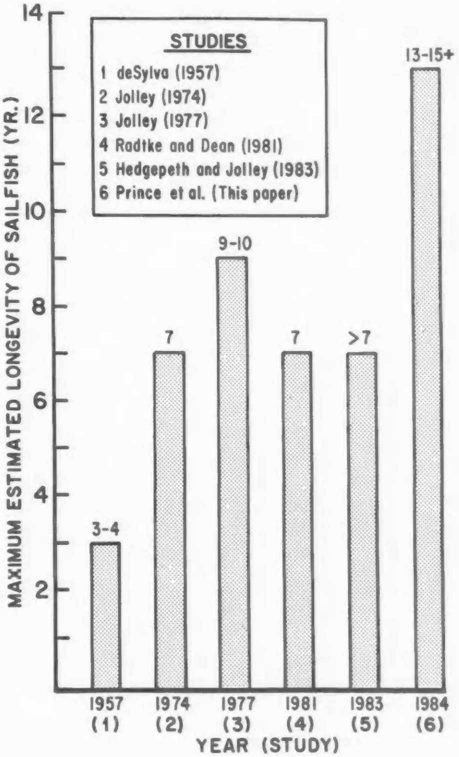

FIGURE 1.—Estimates of maximum longevity (yr) for Atlantic sailfish from six different studies, 1957-84.

grow very slowly after sexual maturity (sexual maturity for female Atlantic sailfish reported at 13-18 kg, Jolley 1977). For example, tagging records indicate that this fish, which was tagged at 18.2 kg, gained only about 6.4 (14 lb) while being at-large almost 11 yr. Our analysis of spines and otoliths support these findings.

Dorsal Spines

Examination of sections from dorsal spines 3-6 (Fig. 2) indicated that the vascularized core comprised an extensive area in all sections. The solid bone area where zonations were not disrupted varied in size and comprised 14, 19, 30, and 37% of the right lobe of spine sections 3, 4, 5, and 6, respectively (Table 1). The vascularized core severely restricted the zonation counts because increments associated with early growth history were totally disrupted and could not be enumerated. Counts of zonations on the four spine sections ranged from 2 to 8 (Table 1). This suggests that spine number 4, which had been used in past studies to assign ages, may not necessarily be the best choice for ageing sailfish, particularly for the larger, older specimens. For example, spines 5 and 6 both had a higher percentage of solid bone, and counts of zonations in these spines were proportionately higher than in spines 3 and 4 (Fig. 2, Table 1). However, all spines substantially underestimated the age of this sailfish, where approximate age (13-15+ yr) was known from tagging records. Hedgepeth[6] reports that spine number 4 would not have been included in the data sets of previous published studies because of the extensive size of the vascularized core area. We conclude from these data that dorsal spine sections are probably only useful for ageing sailfish from >1 to 5 yr. Although there may be some bias associated with ageing these young sailfish because of the vascularized core, this bias is probably minimal. However, for sailfish older than estimated age 5 and about $\geqslant$22.7 kg (50 lb), the bias substantially underestimates age and this bias increases with an increase in size and age of the fish. In addition, spines have not been shown to be useful in ageing sailfish <1-yr-old (Jolley 1974, 1977).

TABLE 1.—Mean count of zonations (3 repetitions) and percentage solid bone in the distal portion of the right lobe of sections taken from dorsal spines 3-6 of Atlantic sailfish (see text and Fig. 2). Measurements and counts were taken along a straight line counting path bisecting the spine laterally from the focus to the edge of each section.

Dorsal spine number	Mean count (range)	Solid bone (%)	Solid bone measurement (mm)	Total measurement (mm)
3	2.0	14	1.89	13.52
4	3.7(3-4)	19	3.55	18.76
5	5.0	30	4.90	16.56
6	7.3(7-8)	37	6.08	16.39

Otoliths

Sagittae from the tagged Atlantic sailfish had external and internal morphologies that were characteristic of sailfish reported by Radtke and Dean (1981), as well as other istiophorids (Radtke et al. 1982; Wilson and Dean 1983; Radtke 1983). For example, major features of these sagittae include a rostrum and antirostrum separated by a deep sulcus (Fig. 3). The external ventral and lateral surfaces of the rostrum consist of a series of ridges that are perpendicular to the axis of growth (Fig. 4). Radtke and Dean (1981) suggested that the number of rostral ridges can be used to estimate age of Atlantic sailfish. To make an accurate count of external ridges for age estimation, it is necessary to understand the internal and external otolith growth pattern so that the location and number of the first few rostral ridges can be firmly established. These initial ridges are often covered by excess calcium carbonate (Wilson 1984), particularly in older specimens, and are not always visible on the external features of the lateral surface (Fig. 4).

The growth of the rostrum occurs in two directions (Figs. 3, 4). During early stages, incremental growth of the rostral lobe occurs in the ventral direction out to a bend where growth shifts to a more medioventral and then to a medial direction (Fig. 3). This same pattern of otolith growth has been reported for blue marlin, *Makaira nigricans*, and white marlin, *Tetrapturus albidus* (Wilson 1984). However, it is difficult to illustrate a complex three-dimensional otolith on a two-dimensional photograph. Therefore, Figures 3 and 4 should be examined consecutively to obtain a proper orientation of the structure.

Although rostal ridges on the external lateral surface (Fig. 4) are not distinct because of the excess calcium carbonate, after the change in the axis of growth, the ridges on the ventral surface (ridges 3-10) can be counted easily (Fig. 4). Several lines of evidence points towards the first two growth zones occurring within the boundaries of the lateral surface. For example, a distinct internal translucent

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[6] Hedgepeth, M. Y., Fisheries Biologist, Florida Department of Natural Resources, 727 Belvedere Rd., West Palm Beach, FL 33405, pers. commun. 1984.

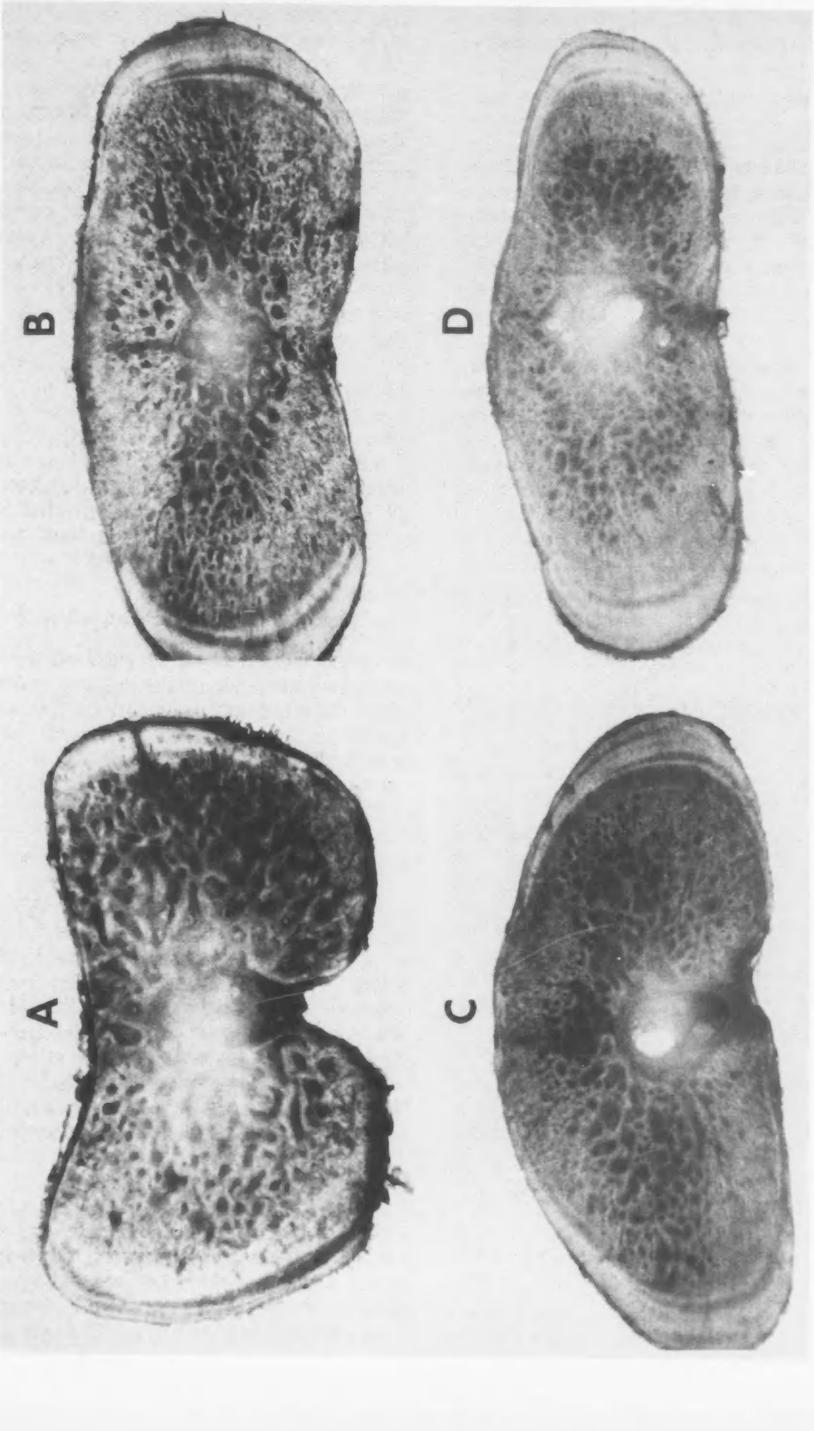

FIGURE 2.—Sections of dorsal spines 3(A), 4(B), 5(C), and 6(D) from a tag-recaptured Atlantic sailfish at-large for 10 yr, 10 mo. Age based on tagging records was 13-15+ yr.

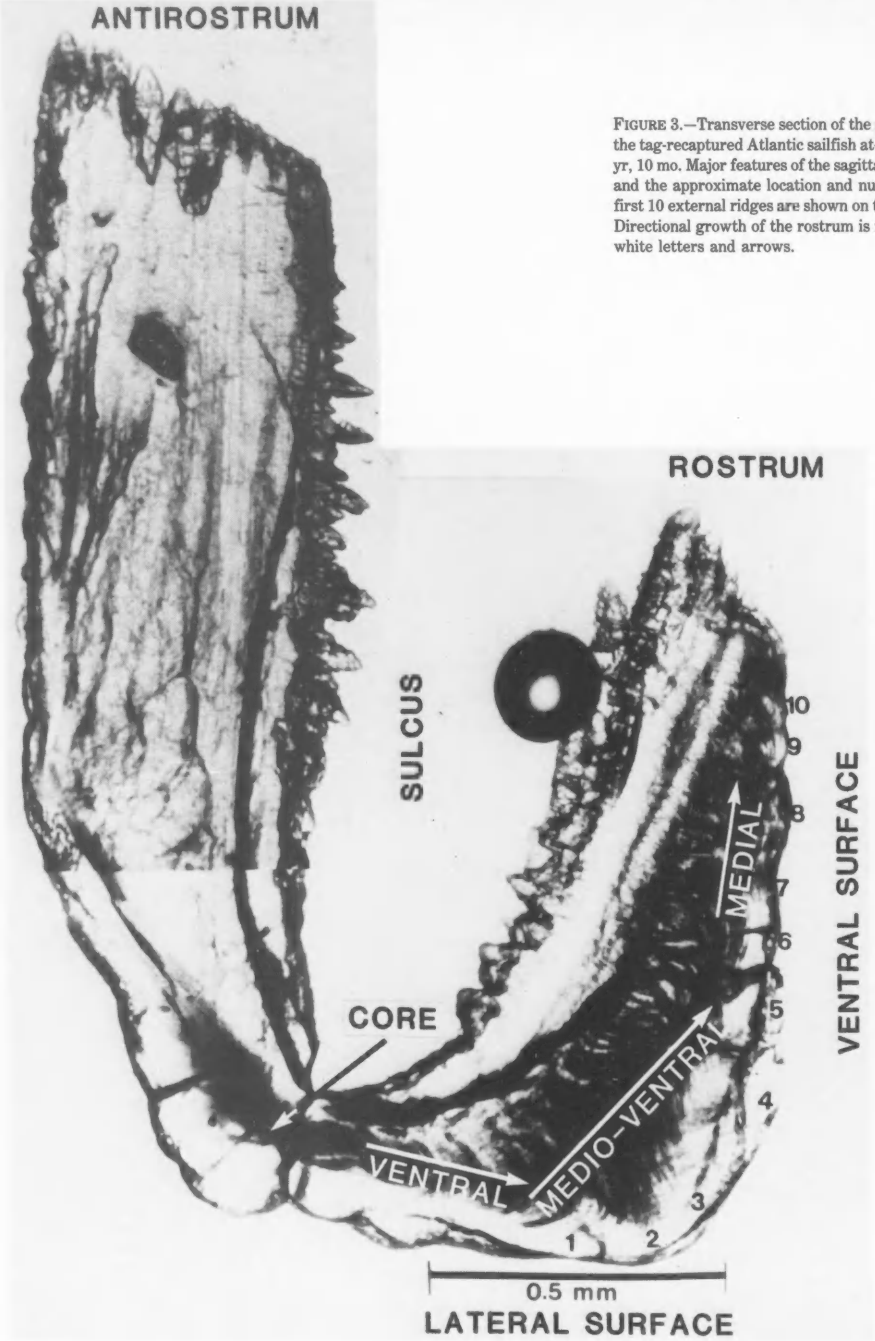
ANTIROSTRUM
ROSTRUM
SULCUS
10
9
8
7
6
5
4
3
2
1
MEDIAL
MEDIO-VENTRAL
VENTRAL
CORE
VENTRAL SURFACE
0.5 mm
LATERAL SURFACE

FIGURE 3.—Transverse section of the sagitta from the tag-recaptured Atlantic sailfish at-large for 10 yr, 10 mo. Major features of the sagitta are labeled and the approximate location and number of the first 10 external ridges are shown on the rostrum. Directional growth of the rostrum is indicated by white letters and arrows.

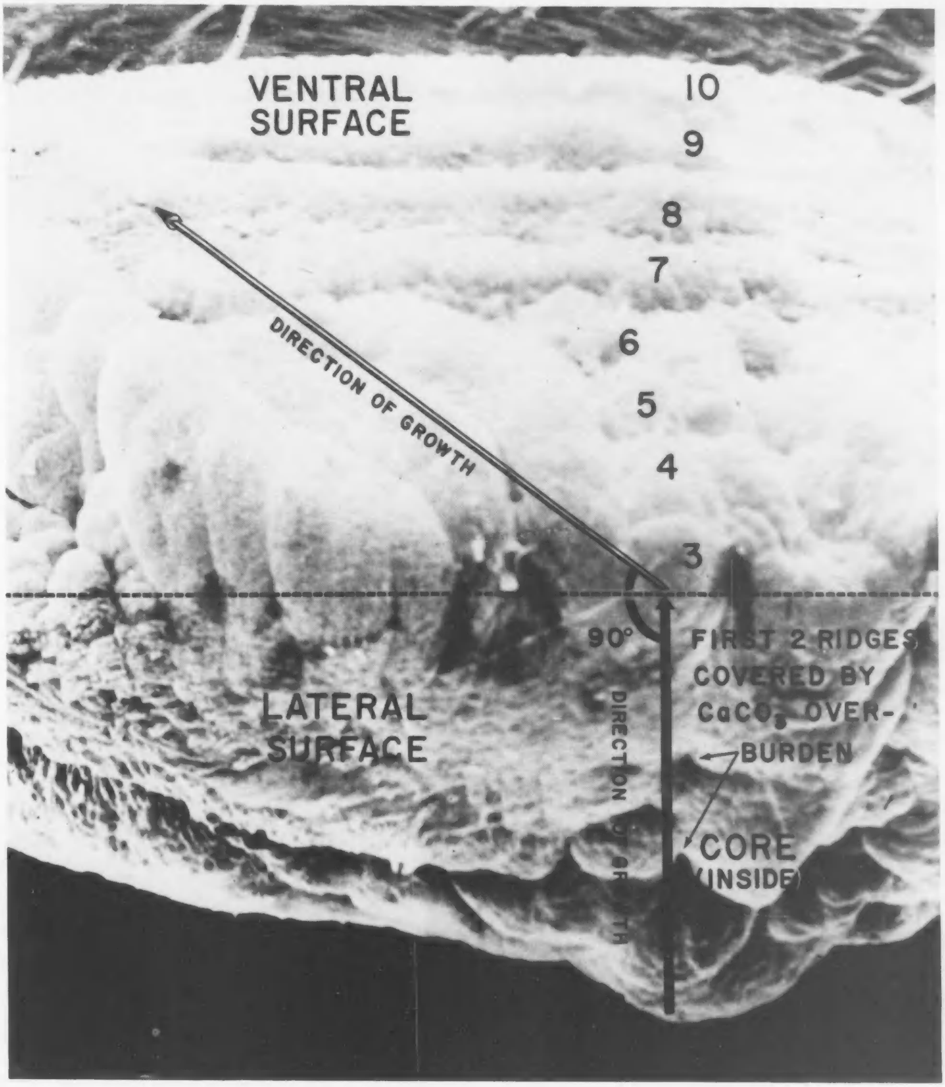
VENTRAL SURFACE
10
9
8
7
6
5
4
3
DIRECTION OF GROWTH
90°
FIRST 2 RIDGES COVERED BY CaCO3 OVER-BURDEN
LATERAL SURFACE
DIRECTION OF GROWTH
CORE (INSIDE)

FIGURE 4.—Lateral and ventral view of the sagitta rostrum from the tag-recaptured Atlantic sailfish showing the overall pattern of otolith growth and the approximate location and number of the first 10 external ridges.

zone exists between the boundary of many of the external ridges shown in Figure 3. This zone extends from the surface to deep within the internal structure of the rostrum (Fig. 3). The distinct change in optical density of the first of these prominent zones marks what we believe is the boundary between the 1st and 2d ridges and suggests that the first major growth zone is located between the core and the bend (Fig. 3). Further, using the SEM we counted 150-200 finely spaced increments between the core and the first prominent translucent zone. This count also supports our interpretation of the location of the first annual zone if these increments are assumed to form daily, the fish was born sometime in late spring or early summer (as reported by Beardsley et al. 1975), and the annual zonations are being formed in the winter. Jolley (1977) reported that annual zones in Atlantic sailfish spines tend to be formed in late fall or winter and he also speculated that sailfish may form the first annuli on spines prior to a full year's growth. The location of the second translucent zone, based on similar evidence, appears to be at the beginning of the bend (Fig. 3). The width of the first two major growth zones (⩾0.5 mm) are considerably larger than the zones beyond the end. Wide spacing of year marks during early growth have been observed in many fishes when growth rates are most rapid (Dean et al. 1983). Therefore, these data support our contention that at least two ridges should be accounted for as occurring within the boundaries of the lateral surface.

Rostral ridges 3 through 10 were easily distinguished and counted on the sagitta's ventral surface within the same plane of focus (Fig. 5, bottom). After the 10th ridge, however, the rostrum changes direction slightly (Fig. 3), and it was necessary to refocus to observe ridges 11 through 13 (Fig. 5, top). We feel that potential sources of error in our counts of rostral ridges would have most likely occurred at the beginning and end of the counting path. In addition, we feel that if errors were made at these locations, they would have increased the count. Therefore, otolith age of the tagged Atlantic sailfish was estimated to be 13 yr. However, it should be recognized that potential errors in this estimate could have resulted if one or two ridges were unaccounted for on the lateral surface or on the tip of the rostrum on the ventral surface. Otolith age under these circumstances should be presented conservatively as ranging from 13 to 15+ yr.

The weight of one sagitta from the tagged Atlantic sailfish (7.84 mg) was extremely heavy for an istiophorid of comparable size. For example, it was 1.24 mg heavier than the sagitta from a 29.6 kg (65 lb) sailfish caught in 1985 off Miami and was 1.18 mg heavier than the largest sagitta from Pacific blue marlin reported by Radtke (1983). In addition, the tagged sailfish sagitta was in the upper range in weight (0.51-8.16 mg) of more than 500 blue and white marlin sagittae examined by Wilson (1984). Since the relationship between the size of otoliths and the age of fishes has been shown to be positively correlated for some teleosts (Somerton 1985), we feel that the relatively large size of this sagitta provides additional indirect evidence that this structure could be from a very old sailfish.

CONCLUSIONS

Our tagging records indicate that estimates of maximum longevity for Atlantic sailfish should be revised upwards to at least 13-15+ yr, and that sailfish of this age can grow at a very slow rate (about 0.59 kg/yr during its time at large). Dorsal spines do not appear to be an accurate source of age and growth information for older, larger sailfish (⩾5 yr, ⩾22.7 kg or 50 lb), while sagittae do provide more accurate estimates of age for these older age groups. Since current stock assessments of Atlantic sailfish (Conser 1984) rely exclusively on dorsal spine ageing data as input, these assessments offer little insight into the more mature segments of the population. If skeletal structures from the larger, older fish are systematically rejected for ageing analyses, an underestimate of age and longevity and an overestimate of growth rate can occur (Nammack et al. 1985). Therefore, future assessments should be revised using otolith ageing methods to clarify that portion of the age structure that can not be reliably appraised using dorsal spines.

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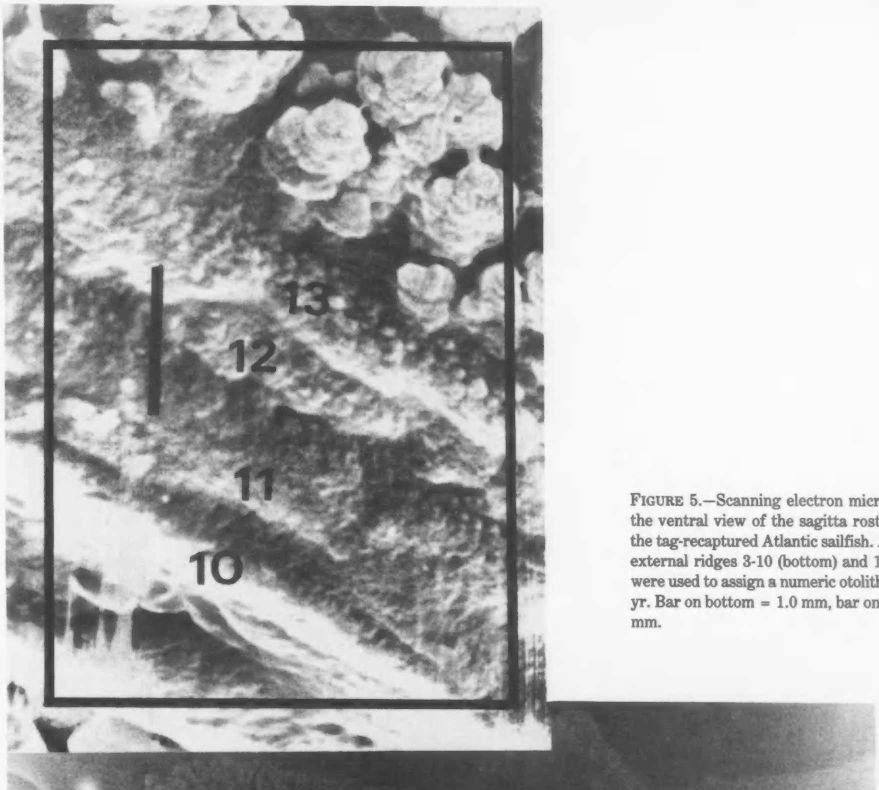

FIGURE 5.—Scanning electron micrograph of the ventral view of the sagitta rostrum from the tag-recaptured Atlantic sailfish. A count of external ridges 3-10 (bottom) and 10-13 (top) were used to assign a numeric otolith age of 13 yr. Bar on bottom = 1.0 mm, bar on top = 0.1 mm.

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AGE DEPENDENT FECUNDITY, NUMBER OF SPAWNINGS PER YEAR, SEX RATIO, AND MATURATION STAGES IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

Richard H. Parrish,[1] Donna L. Mallicoate,[1] and
Richard A. Klingbeil[2]

ABSTRACT

Maturity stage data from fishery sampling programs and ovarian histological data from research cruises were used to develop a method for determining the age-specific number of spawnings per year and annual fecundity of the central stock of northern anchovy, *Engraulis mordax*.

The sex ratio was found to be size and age dependent in both the fishery and trawl surveys with females increasingly dominant in the larger and older size and age classes. The overall sex ratio in trawl surveys was nearly 1:1; the fishery data favored females 1.48:1. The magnitude and duration of maturity stages were size and age dependent with peak spawning occurring earlier in the season in younger fish. Maturity stages and histological classes with hydrated eggs showed essentially the same diurnal pattern for nightly spawning activity indicating that the presence of hydrated eggs could be used as an index of daily spawning. The daily spawning incidence and total annual fecundity were found to be heavily age dependent. Females in their first spawning season had an average of 5.3 spawnings, while those in their fourth had an average of 23.5 spawnings. When combined with the higher batch fecundity of larger fish this results in 4+ year-old females producing nearly 5 times as many eggs per unit of weight as 1-year-olds. When the age-specific fecundity and sex ratio in the fishery are combined it is apparent that the catch of a ton of 4+ year-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-year-olds.

It was concluded that age-specific fecundity in multiple spawning fishes is of greater significance for management than previously thought. It is also significant that much of the observed variance in stock-recruitment relationships for multiple-spawning fishes may be due to the fact that spawning biomass is a poor index of the egg production and reproductive potential of the stock.

Age-specific variation in life history rates is a major factor in population and management models of exploited fishes, and variation in reproductive effort is of great significance in such models. Size and age-specific batch fecundity estimates have been available for many species for decades, and for species which spawn only once per spawning season these are readily incorporated into models. However it has been impossible to determine the age-specific reproductive effort of species which spawn many times during a spawning season because there has been no way to determine the number of spawnings per year.

Recent research on the histology of the ovaries of northern anchovy, *Engraulis mordax*, and anchoveta, *Engraulis ringens*, suggest that they spawn approximately once a week during peak spawning months (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Alheit et al. 1983; Alheit et al. 1984). Hunter and Leong (1981), in their study of the spawning energetics of the northern anchovy, found that northern anchovy spawn about 20 times per year. Hunter and Leong (1981) and Alheit et al. (1983) suggested that annual fecundity per unit of parental biomass may be highly variable and dependent upon the nutritional state and size structure of the stock.

Potentially the recently developed histological techniques could be utilized to determine age-specific annual fecundity; however, this would be very expensive as it would require a very large data set which would necessarily be stratified by age and time of year. The objectives of this report are 1) to demonstrate a method for combining the high resolution reproductive information from the histology of the ovaries with inexpensive, lower resolution reproductive information derived from resource surveys and fishery sampling programs to determine the age-specific reproductive potential of a multiple spawning species, and 2) to evaluate the gross anatomical maturity stages which have been

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[1] Southwest Fisheries Center, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942.

[2] California Department of Fish and Game, 245 W. Broadway Street, Long Beach, CA 90802.

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utilized in field sampling programs for northern anchovy and to use the historical data from these programs in conjunction with ovarian histological data to describe age-dependent annual fecundity in the central stock of northern anchovy.

DATA SOURCES

There are three major sources of biological data for adult northern anchovy in California: samples taken from the commercial fishery (Collins and Spratt 1969), samples taken from midwater trawl hauls carried out by the Sea Survey Program (Mais 1974), and samples taken primarily by midwater trawl during egg production cruises (Picquelle and Hewitt 1983). The first two sources are the result of long-term research and monitoring programs carried out by the California Department of Fish and Game, and the third is the result of research cruises carried out by the National Marine Fisheries Service. The fishery data used in this analysis consist of biological information for 60,661 northern anchovy sampled from the San Pedro purse seine fleet during the period of 1966-80 and 4,904 northern anchovy sampled from the Monterey fleet during 1966-78. All northern anchovy in the fishery samples were aged and nearly all were assigned maturity stages. We used a geographically restricted subset of the 1966-83 sea survey data (lat. 29.5°-34.5°N; 54,457 northern anchovy). Maturity stages were not recorded for males in the sea survey data and age determinations were made on only a portion (19,031) of the fish sampled. In both data sets age determinations were made from otoliths with methods described by Collins and Spratt (1969). The third source of data, provided to us by B. Macewicz[3], consists of histological information for the gonads of 8,672 females sampled during the months of February to April from 1977 to 1984. Age determinations were not made and maturity stages were not taken on these fish.

The gross anatomical maturity stage description used for northern anchovy is a slightly modified version of the system developed by Bowers and Holliday (1961) for herring. The system has seven maturity stages which are primarily based on the portion of the body cavity occupied by the gonads and, in the later stages, by the appearance of translucent eggs or milt (Table 1). Herring are considerably larger than anchovy, and they are generally not considered to be multiple spawners; therefore, there are some difficulties in applying the maturity stages to anchovy. The most obvious problem is that a considerable proportion of the anchovy sampled had gonads so small that sex determinations were not made as they would have required magnification. There was also a small proportion of fish in which physical deterioration made sex determination impossible. The California anchovy fishery is primarily for reduction to fish meal, and the quality of the fish was occasionally very poor when the fish were sampled. Another major difficulty is that it is not possible to distinguish between anchovy gonads that are resting (i.e., stage 2) between multiple spawnings in the same season and those resting between spawning seasons. A comparable problem exists with spent fish (stage 7).

TABLE 1.—The international (Hjort) scale of maturity stages of the gonad. From Bowers and Holliday (1961).

Stage 1:	Virgin individuals: very small sexual organs close under vertebral column; ovaries wine-colored, torpedo-shaped, about 2-3 cm long and 2-3 cm thick, eggs invisible to naked eye; testes whitish or greyish-brown, knife-shaped, 2-3 cm long and 2-3 cm broad.
Stage 2:	Maturing virgins or recovering spents: ovaries somewhat longer than half the length of ventral cavity, about 1 cm diameter, eggs small but visible to naked eye; milt whitish, somewhat bloodshot, of same size as ovaries, but still thin and knife-shaped.
Stage 3:	Sexual organs more swollen, occupying about half of ventral cavity.
Stage 4:	Ovaries and testes occupying almost two thirds of ventral cavity; eggs not transparent, milt whitish, swollen.
Stage 5:	Sexual organs filling ventral cavity; ovaries with some large transparent eggs; milt white, not yet running.
Stage 6:	Roe and milt running (spawning).
Stage 7:	Spents: ovaries slack with residual eggs; testes baggy, bloodshot.

SEX RATIO

Description of the sex ratio in northern anchovy was confounded by the presence of fish for which the sex could not be determined. The relationship between size and the percentage of these unsexed fish is similar for both the commercial purse seine and midwater trawl data. In both data sets, a large percentage of the fish smaller than 100 mm standard length (SL) are of unknown sex, about 10% of the 101-110 mm fish are of unknown sex, and only a small percentage of the fish larger than 110 mm are of unknown sex (Table 2). The percentages of fish with unknown sex at sizes larger than 110 mm in the purse seine data are somewhat higher than those in the midwater trawl data. This is probably due to the occasional occurrences of fish in which the condition was too poor to allow sex identification. The relationship between age and the percentage of unsexed fish is similar to that described for size (Table 2). It should be noted that both data sets are biased towards larger and older fish. The age composition of anchovy in the midwater trawl data is biased because of the fact that otoliths were often not taken when trawl hauls were dominated by young-of-the-year fish (Parrish et al. 1985). The purse seine data contain a much smaller percentage of small or young fish than the midwater trawl data. This is primarily caused by the fact that a 5-in (about 108 mm SL) minimum size limit was in effect for most of the 1966-80 period.

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[3] B. Macewicz, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. August 1984.

To evaluate the seasonal cycle of the occurrence of northern anchovy for which the sex could not be identified, the monthly percentages of females, males, and anchovy with unknown sex were determined by age group for the San Pedro fishery (Fig. 1). In all age groups the minimum percentages of fish which could not be sexed occurred from about January to May in association with the spawning season. Higher percentages occurred both before and after the spawning season, particularly in the first potential spawning season. This implies that a significant percentage of anchovy mature, or at least partially mature, and then reabsorb their gonadal tissue to the point that their gonads are so small that they cannot be sexed without magnification. It also implies that a bias due to the unsexed fish exists. This bias is at a minimum from January to May and it primarily affects the analyses of fish in their first potential spawning season.

Klingbeil (1978) found the female:male ratios of northern anchovy sampled in the Sea Survey Program and in the commercial fishery to be 1.03:1 and 1.60:1 respectively. The additional years of information from these two sources, in our data sets, pro-

TABLE 2.—Proportion of northern anchovies with unknown sex and sex ratio by size (A) and by age (B).

	San Pedro anchovy fishery				Sea survey (lat 29.5°-34.5°N)			
Length (mm)	Unknown sex	Females/male	Mean SL	Number	Unknown sex	Females/male	Mean SL	Number
				A				
61- 70	1.000	—	—	1	0.996	0.00	—	273
71- 80	0.676	0.71	—	37	0.941	0.94	—	597
81- 90	0.437	0.67	—	252	0.810	0.78	—	1,396
91-100	0.283	0.77	—	2,261	0.500	0.84	—	2,208
101-110	0.114	1.06	—	8,684	0.100	0.82	—	2,882
111-120	0.057	1.30	—	17,186	0.016	0.78	—	4,141
121-130	0.029	1.53	—	19,396	0.007	1.07	—	4,016
131-140	0.014	2.10	—	10,010	0.003	1.43	—	2,439
141-150	0.007	2.90	—	2,354	0.003	2.56	—	772
151-160	0.009	4.43	—	438	0.005	3.09	—	185
161 +	0.024	7.20	—	42	0.000	9.67	—	32
Total	0.057	1.48	—	60,661	0.187	1.02	—	19,031
				B				
Age				Annual				
0	0.202	0.83	104.2	1,862	0.779	0.81	88.7	3,616
1	0.090	1.15	112.8	16,167	0.122	0.88	107.2	4,812
2	0.046	1.49	121.1	20,885	0.022	0.86	119.4	4,733
3	0.036	1.76	126.3	14,174	0.010	1.15	126.4	3,543
4 +	0.022	2.01	134.0	7,573	0.003	1.66	135.0	2,327
Total	0.057	1.48	121.2	60,661	0.187	1.02	113.7	19,031
Age				February-April				
0	—	—	—	0	—	—	—	0
1	0.093	0.95	106.5	4,646	0.153	0.79	101.0	2,271
2	0.027	1.33	116.2	4,279	0.004	0.78	117.3	2,035
3	0.018	1.45	123.3	3,410	0.002	1.04	125.3	1,928
4 +	0.014	1.69	134.4	3,620	0.001	1.55	134.6	1,382
Total	0.041	1.30	119.0	15,955	0.048	0.96	117.6	7,616
Age				August-December				
0	0.259	0.77	104.2	1,204	0.831	0.78	88.6	3,216
1	0.083	1.19	117.6	6,411	0.104	0.97	112.2	2,198
2	0.060	1.59	123.1	12,082	0.035	0.91	120.5	2,311
3	0.051	1.92	127.7	7,648	0.021	1.28	128.1	1,255
4 +	0.039	2.33	132.9	2,532	0.007	1.57	135.4	560
Total	0.069	1.58	123.2	29,877	0.316	1.02	109.7	9,540

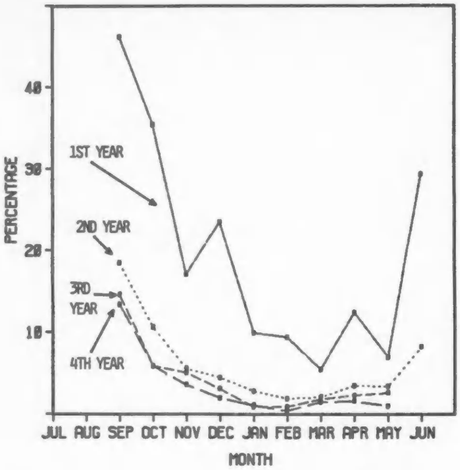

FIGURE 1.—The monthly percentages of northern anchovies with unknown sex, by age group, in samples from the San Pedro fishery.

duced essentially no change in the sex ratio in the sea survey data (1.02:1). However, there was a reduction in the proportion of females in the fishery data (1.48:1) which was associated with a reduction in the average age of anchovy in the catch after 1977 (Mais 1981). Sunada and Silva (1980) also found a female:male sex ratio greater than unity in the northern Baja California purse seine fishery, 2.15:1 in 1976 and 1.44:1 in 1977. Alheit et al. (1984) reported a sex ratio of 1.30:1 in purse seine caught Peruvian anchoveta sampled during their spawning season. Klingbeil (1978) and Alheit et al. (1984) reported that during the spawning season there were unexpectedly large numbers of samples in which sex ratios were heavily dominated by either males or females. Alheit et al. (1984) suggested that "hydrated females segregate, either by depth or area, from the 'normal' school, taking a high percentage of males with them forming 'spawning schools' dominated by males."

Analysis of the sex ratio by size and age groups shows that there are increasingly larger proportions of females in the larger and older groups (Table 2). This trend is evident in both the fishery and sea survey data. In the fishery data there are more males than females identified in the fish smaller than 100 mm SL and in age group 0. The proportion of females increases until there are more than twice as many females as males among fish larger than 130 mm and in age group 4+. There is a similar trend in the sea survey data; however, females do not outnumber males until the fish are larger than 120 mm and 3 yr of age. The sex ratio in age group 4+ is 1.66:1. The apparent dominance of females in the larger size classes may be partially caused by sex related differences in growth rates; however, their dominance in the older age classes of both the purse seine and midwater trawl samples cannot be explained by differences in growth. We grouped our data sets into the spawning months (February-April) and nonspawning months (August-December) in order to evaluate features which might be caused by behavioral differences that may occur during the spawning season. This analysis shows that the overall sex ratio in northern anchovy taken by midwater trawl is close to 1:1 in both nonspawning and spawning seasons (Table 2B). It also shows that the sex ratios in younger fish are dominated by males and those in older fish are dominated by females. The overall sex ratio in northern anchovy sampled in the purse seine fishery is heavily dominated by females; however, the sex ratio is higher in the nonspawning season (1.58:1) than in the spawning season (1.30:1). The crossover from male to female dominance of the sex ratio occurs between age group 2 and 3 in the sea survey data and at age 1 in the fishery data.

MATURITY STAGES IN NORTHERN ANCHOVY

Seasonal Variation in Maturity Stages

To determine which of the various data sets available for northern anchovy were best suited for evaluating maturity stages in the central stock, we examined the seasonality of three grouped maturity stages of four data subsets. The grouped stages included immature or resting females (stages 1 and 2); females just beginning to mature (stage 3); and the highly mature, spawning, and spent females (stages 4-7). The data consisted of two sets of samples from the commercial fishery (Monterey and San Pedro) and the sea survey samples from southern California (lat. 32.5°-34.5°N) and northern Baja California (29.5°-32.5°N).

The seasonal patterns of the grouped maturity stages of females sampled in the San Pedro fishery (Fig. 2A), the sea survey in southern California (Fig. 2B), and the sea survey in northern Baja California (Fig. 2C) are quite similar. The pattern in the Monterey fishery differs from that in the other data sets in that spawning is at the highest levels in April and September (Fig. 2D). It cannot presently be determined if there are one or two peaks of spawning in

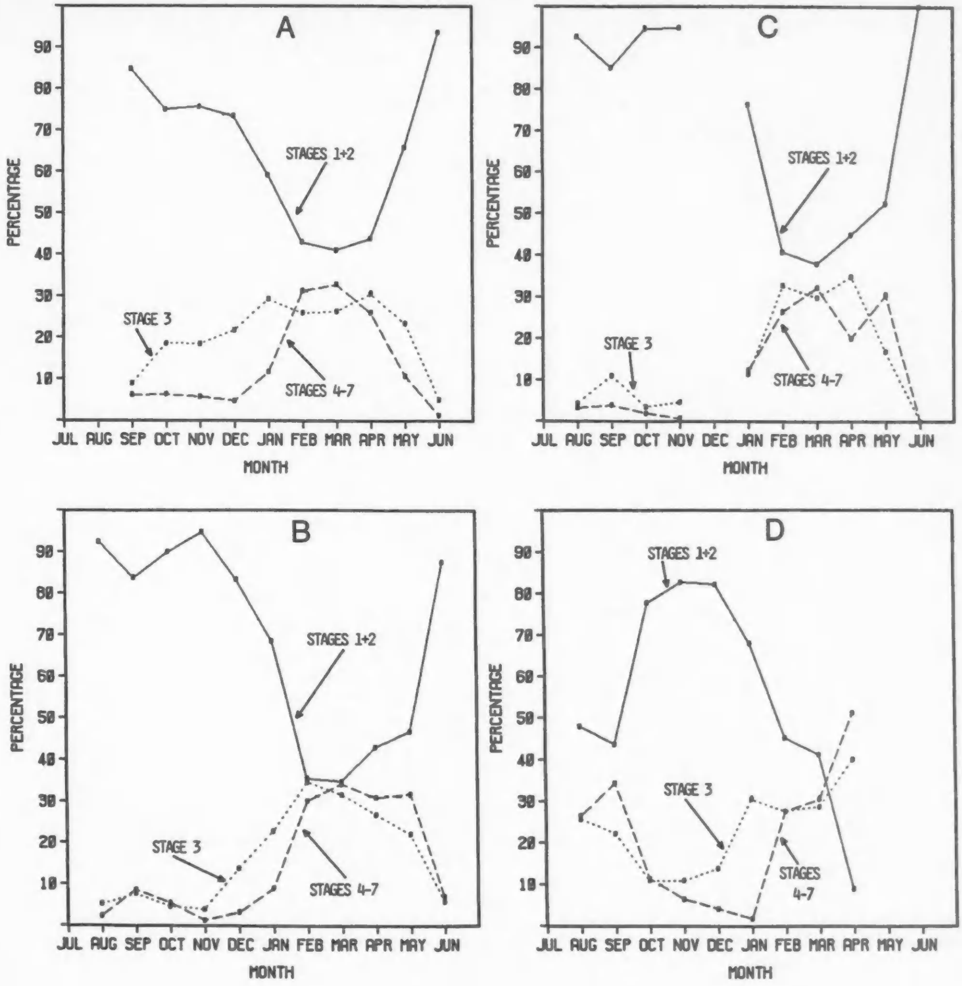

FIGURE 2.—The monthly percentages of grouped maturity stages for female northern anchovies sampled in A, San Pedro fishery; B, Sea survey (lat. 32.5°-34.5°N); C, Sea survey (29.5°-32.5°N); D, Monterey fishery.

the Monterey area due to the lack of data from May to July. Because of the different seasonal pattern of the grouped maturity stages in the Monterey fishery data and because there is more than one stock in this region (Vrooman et al. 1981), it was decided to exclude this area from further analysis. The analyses that follow are based on the combined San Pedro fishery and southern California-northern Baja California sea survey data sets (52,352 females of which 41,930 were aged).

To obtain a first approximation of the magnitude and duration of maturity stages in the central stock of northern anchovy, the monthly percentages of fish with each maturity stage were calculated for females and for males. The seasonal patterns were found to be essentially the same for males and females; however, the males tended to have somewhat larger percentages of fish in the higher maturity stages. Our presentation is limited to information on females.

The proportion of females classified as stage 1, virgin individuals, is at a minimum during the spawning season, comprising <10% of the females sampled during February, March, and April. However, during the summer more than half of the females were classified as stage 1 (Fig. 3A). Stage 2 females, maturing virgins and recovering spents, are at a minimum in August (when most females are classified as stage 1). From September until January between 40 and 60% of the females are classified as stage 2. During the spawning season, and just after, the percentage of stage 2 females dropped between 30 and 40%. The August to September decline in the percentage of stage 1 females is primarily caused by the sharp increase in the proportion of stage 2 females. Thus, the combined percentage of stages 1 and 2 females is probably a reasonable inverse indicator of the seasonality of spawning. However, during the spawning season an unknown proportion of those classified as stages 1 and 2 are females that have recently spawned and are between multiple spawnings.

Stage 3 females (ovary enlarged, occupying about half of the length of the ventral cavity) have a considerably different pattern. There is a gradual increase from about 5% in August to about 30% in January. This percentage is maintained until April, i.e., through the spawning season; it then drops to about 5% in June. The monthly percentages of the higher maturity stages (4, 5, and 6) clearly delineate the spawning season as primarily a January-May event (Fig. 3B). The relatively constant low level of stage 7 females is unexpected as the maximum proportion of spent fish would be expected to occur just after the peak of spawning.

Maturity Stage Relationships with Size and Age

To examine potential relationships between the size and age of northern anchovy and the duration and magnitude of maturity stages we calculated the monthly percentages of grouped maturity stages for four size classes (81-100, 101-120, 121-140, and 141-160 mm SL) and four age groups (1, 2, 3, and 4+). Age group 1 includes fish prior to and after their first potential spawning season (i.e., young-of-the-year fish in July through the following June). Age group 4+ includes fish in their fourth and subsequent spawning seasons. The grouped maturity stages (1, 2, 3, and 4-7) are the same as those presented earlier.

Size has a large effect on both the duration and magnitude of maturity stages in northern anchovy. With the exception of those sampled from February to April nearly all of the 81-100 mm SL females were classified as immature or resting (Fig. 4A). In addition, the majority of this size anchovy have gonads too small to determine their sex without magnification (Table 2). As the size class increases the percentage of stages 1 and 2 decreases; this occurs in all months; however, the minimum percentage of

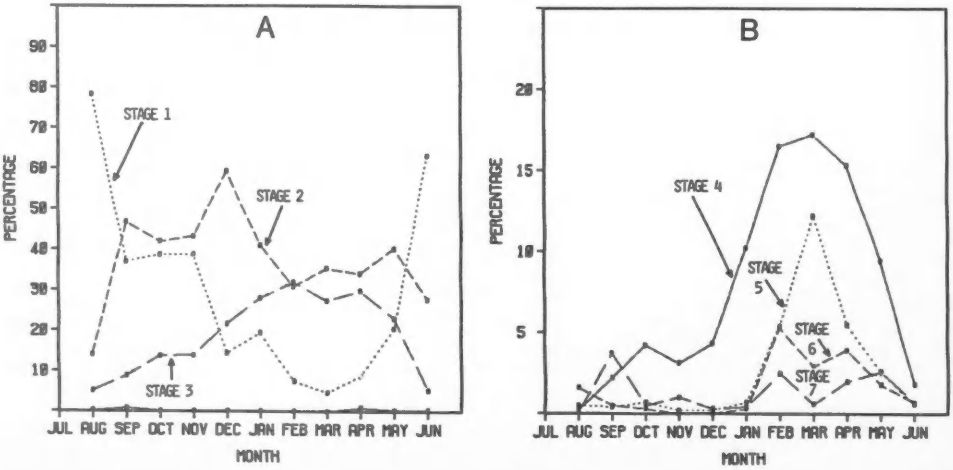

FIGURE 3.—The monthly percentages of individual maturity stages for female northern anchovies. A. Stages 1-3. B. Stages 4-7.

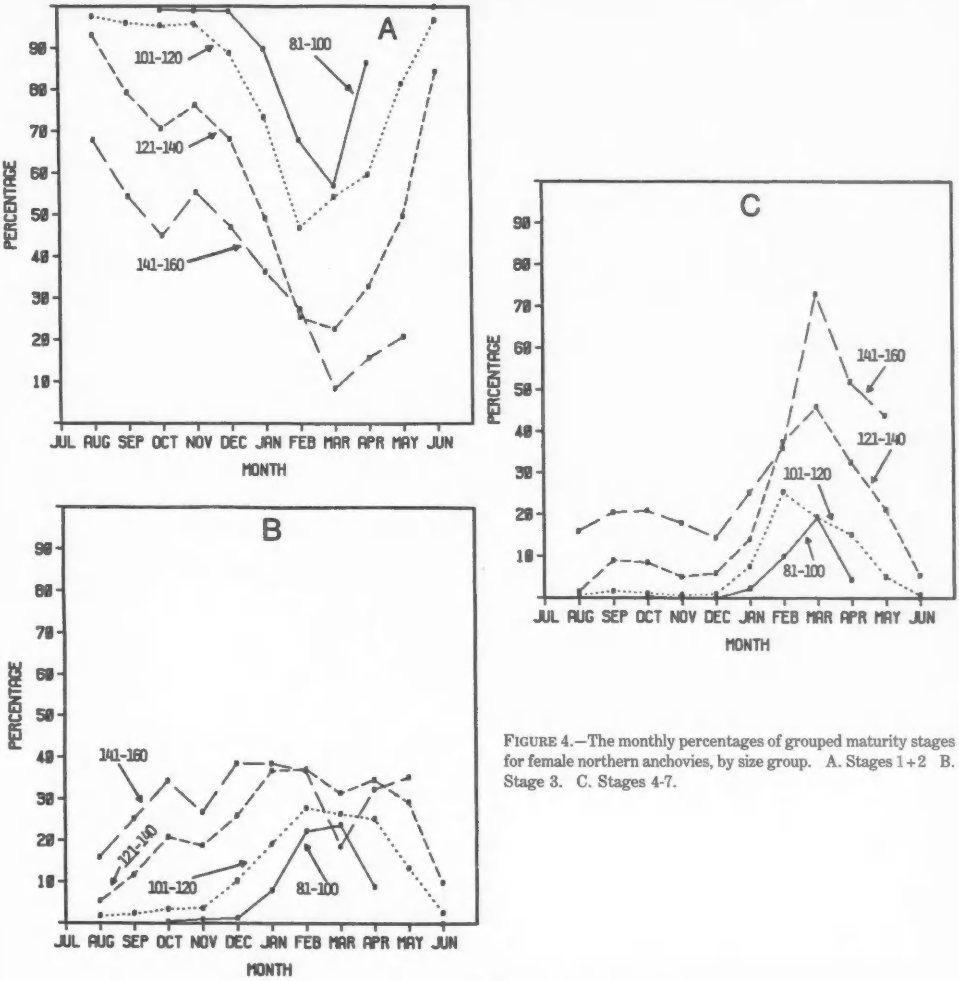

FIGURE 4.—The monthly percentages of grouped maturity stages for female northern anchovies, by size group. A. Stages 1+2 B. Stage 3. C. Stages 4-7.

stages 1 + 2 occurs in February to April. The percentage of females just beginning to mature (i.e., stage 3) has an abrupt peak in February-March in the smallest size class (Fig. 4B). This peak becomes increasingly spread out in the larger size classes. The higher maturity stages (4-7) are most abundant from February to April in all size classes (Fig. 4C). The larger size classes have much larger percentages of females in the higher maturity stages than the smaller size classes, and there is a minor peak in the percentage of the higher maturity stages during the fall in the two largest size classes. Analysis of the data by age group showed, as would be expected, that increased age has essentially the same effect as increased size on the magnitude and duration of maturation stages.

SPAWNING INCIDENCE AND FECUNDITY

Studies by Hunter and Goldberg (1980) in California and Alheit et al. (1983) in Peru examined postovulatory follicles to determine the spawning frequency of female anchovies (i.e., the time interval between spawnings). A second method would be to determine the percentage of females with hydrated eggs. Hunter and Macewicz (1980) showed that northern anchovy begin hydrating eggs at about 0600 in the morning and by sunset about 14% of the females have hydrated eggs. They felt that the best indicator of the time of spawning was the occurrence of both hydrated eggs and new postovulatory follicles. This occurred in a low percentage of their samples indicating that spawning was completed rapidly; the time of maximum spawning occurred between 2100 and 0200 with a peak between 2200 and 2300. Hunter and Macewicz (1980) divided the nightly pattern of spawning in anchovy into three periods: "early spawning period (1800 to 2100 hours), some spawning occurs but the ovaries of most reproductively active females are in the hydrated stage; maximum spawning (2100-0200 hours), most females spawn (females with hydrated eggs decline to 0 and females with new postovulatory follicles reach the maximum number for the night); and post-spawning (0200-0600 hours), little or no spawning occurs and females destined to spawn the next night begin hydration." A considerable amount of new histological data is now available as a result of a series of egg production biomass surveys for northern anchovy. B. Macewicz (fn. 3) has analyzed the histology of the ovaries of 8,672 anchovy sampled in these surveys, and our analysis of this new information verifies the temporal patterns which Hunter and Macewicz (1980) described from a much smaller sample (Fig. 5).

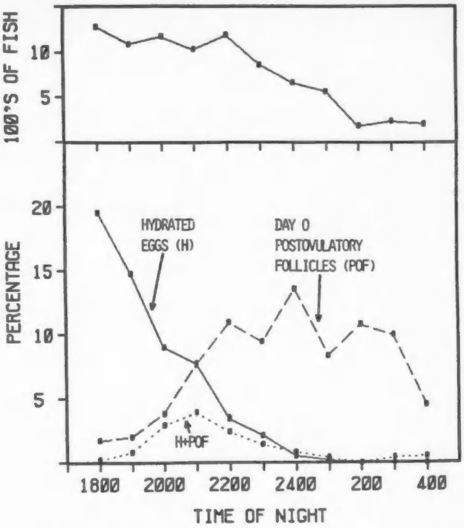

FIGURE 5.—The percentages of female northern anchovies with ovaries in three histological classes, by time of night.

Comparison of Maturity Stages and Histology Classes

The histological data show that during the early evening the percentage of females with hydrated eggs could be an indicator of the percentage of females spawning per day (i.e., the spawning incidence). To use the extensive maturity stage data available for northern anchovy it is necessary to determine the relationships between the histology of the gonads and the maturity stages used in the California Department of Fish and Game's sampling programs. To date histological and field maturity stage data have not been taken on the same individuals; therefore, analysis is limited to comparisons of the two data sets. In the following comparisons the sea survey and histology data sets were limited to samples taken during the period 1977-84 and during the principal spawning season (i.e., February-April). Since nearly all of the trawls were taken at night, the data were limited to those taken from 1800 to 0500 h. The midwater trawl hauls were normally 15 min in duration, and about 30% of the fish in the histological data set and 30% in the maturity stage data sets were taken in the same trawl hauls during cooperative cruises.

The histological data are divided into six classes (B. Macewicz fn. 3):

1. Ovaries with hydrated eggs and no day-0 postovulatory follicles.
2. Ovaries with hydrated eggs and day-0 postovulatory follicles.
3. Ovaries with day-0 postovulatory follicles and no hydrated eggs.
4. Ovaries with day-1 postovulatory follicles.
5. Mature ovaries with no hydrated eggs, no day-0 nor day-1 postovulatory follicles.
6. Immature ovaries, few or no yolked oocytes, no atresia present in the ovary other than late-stage corpora atretica.

Northern anchovy, spawning on the night they were sampled (day 0), include the first three classes; those that spawned on the night before they were sampled (day 1) are class four.

A comparison of the percentages of hydrated females in the sea survey data (i.e., stages 5 + 6) with that in the histological data (i.e., classes 1 + 2) shows that they have essentially the same pattern from the onset of spawning in the early evening until spawning is completed in the early morning (Fig. 6). This implies that in the early evening maturity stages 5 + 6 can be used to estimate the spawning incidence; however, within a few hours after sunset the percentage of females with hydrated eggs (i.e., stages 5 + 6) rapidly becomes an underestimate of the incidence of spawning due to the completion of spawning. If only the females (n = 2,161) sampled between the hours of 1800 and 2000 are considered, then the percentage in maturity stages 5 + 6 (15.3%) is quite close to the percentage of day-0 females calculated for the total histology data set (15.9%).

The variation throughout the night of the percentages of the other maturity stages is also of interest as it offers some insight into the meaning of maturity stages in anchovy. Hunter and Macewicz (1980) showed that spawning primarily occurs between the hours of 1800 and 0200. In the sea survey data the percentage of stages 5 + 6 falls from 15.3 to 1.6% over this time period (Fig. 7). The expected maturity stage that should increase over this time period is stage 7 (i.e., spents: ovaries slack with residual eggs). This, however, is not the case. The percentage of stage-7 females has very little variation over the 1900-0200 period; going from 2% at 1900 to 3.6% at 0200. This suggests that residual eggs occur in only a small percentage of anchovy and that stage 7 cannot be used to determine if an anchovy has spawned within 24 h. This is consistent with Stauffer and Picquelle's (1980) observation that field-spawned northern anchovy were found to release nearly 100% of their hydrated eggs. The percentages of the other maturity stages show considerable variation from 1900 to 0200 h. Stages in which the ovary is small (i.e., 1+2) occur in about 37% of the females in the early evening. This increases rapidly after 2300 and by 0200 these stages comprise about 46% of the females. Stages 3 + 4, in which the ovaries occupy from one half to two thirds of the ventral cavity, occur in about 46% of females in the early evening. This rises to a peak of about 54% at 2300-2400 and then declines to about 49% at 0200.

Our interpretation of the patterns exhibited by the sea survey data is that the percentage of females at stages 5 + 6 in the early evening (i.e., 15.3%) is a valid estimate of the percentage of sampled females with hydrated eggs. However, as the night progresses the percentage of stages 5 + 6 declines. At the peak of spawning, just before midnight, many females appear to be misidentified as stages 3 + 4. This could occur if they had spawned part of their eggs before they were captured and if the person making the maturity stage determinations used the size of the ovary, rather than the presence of hydrated eggs, to determine the maturity stage. After midnight an increasing percentage of spawning females have

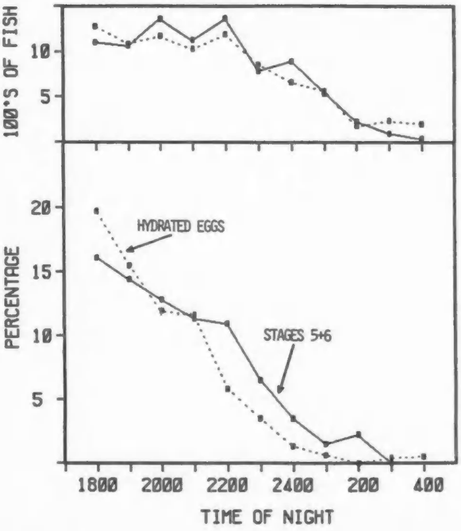

FIGURE 6.—The percentages of female northern anchovies with hydrated eggs and with maturity stages 5+6, by time of night.

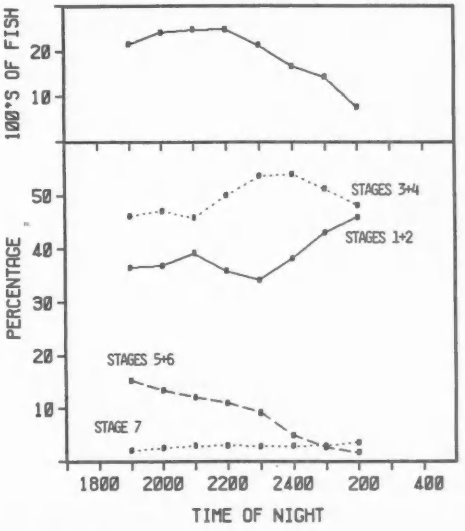

FIGURE 7.—The percentages of grouped maturity stages for female northern anchovies by time of night. (Two hour moving average.)

apparently spawned all of their hydrated eggs and they are then classified as stage 1 or 2. The meaning of stage 7 in female anchovy remains a mystery.

The seasonal and diurnal patterns described above indicate that, with the exception of stages defined by the presence of hydrated eggs, gross anatomical maturity stages have little utility other than describing the seasonality of spawning. However, field identifications of the presence of hydrated eggs, if they are calibrated with histological data and if the diurnal pattern of hydration is known, can potentially be used to determine spawning incidence.

Several authors have pointed out that females with hydrated eggs and actively spawning females were more numerous than females with day-1 postovulatory follicles, and have suggested that hydrated and actively spawning females may be more susceptible to capture due to behavioral or physiological factors (Hunter and Goldberg 1980; Stauffer and Picquelle 1980; Alheit et al. 1984). Previous workers have therefore used the percentage of day-1 females as the index of the daily spawning incidence. The overall percentages of day-0 and day-1 females in the histology data set (8,672 females) used in our analyses are 15.9 and 11.5%. Alheit et al. (1983) found the overall percentages of day-1 and day-2 Peruvian anchoveta females to be 17.26 and 14.81%. Hunter and Goldberg (1980), and subsequent workers on the northern anchovy, took their samples at night whereas Alheit et al. (1983) took their Peruvian anchoveta samples primarily during the day. Therefore the definition of day-1 is somewhat different in studies of the two species. In our analysis both day-0 and day-1 females appear to be more susceptible to capture by midwater trawl in the early evening than later at night. The percentages of both decline as the night progresses; however, the decline is more extreme in the day-0 females (Fig. 8).

The use of maturity stages 5 + 6 could result in several sources of bias that would tend to produce overestimates of the spawning incidence of northern anchovy. If females with hydrated eggs are more susceptible to capture, there will be a tendency to produce biased estimates. However, this bias would not be expected to be size or age dependent, nor would it be expected to vary during the spawning season. The same bias would be expected to occur in 1- and 4-yr-old hydrated females and the same bias would be expected in February and April. Therefore the use of the percentages of hydrated females or maturity stages 5 + 6 females may result in overestimates of the total spawning incidence or annual fecundity, but the relative spawning incidence or relative annual fecundity of the different age groups would not be biased. A second source of bias is that an unknown number of females have ovaries so small that visual determination of sex is impossible without magnification. Therefore, the incidence of spawning is overestimated because it is calculated by dividing the number of stages 5 + 6 females by less than the total number of females. This bias is size and age dependent, being much more common in smaller and younger anchovy, but not month dependent. Note that the various studies of the spawning incidence in northern anchovy and Peruvian anchoveta have defined the spawning incidence to be the number of females spawning per day divided by the number of *mature* females, i.e., these studies exclude immature females, which are primarily the smaller and younger fish, from the calculation.

There are also several sources of bias that would tend to produce underestimates of the spawning incidence. The anchovy fishery in southern California primarily occurs at night during the fall months and during the daylight hours in the spring. A period of low availability to the commercial fishery is associated with the spawning season. Mais (1974) associated this phenomenon with variation in schooling behavior and showed that acoustic surveys detect relatively few "commercial-sized" anchovy schools during the spawning season. If low availability to the commercial fishery is associated with spawning ac-

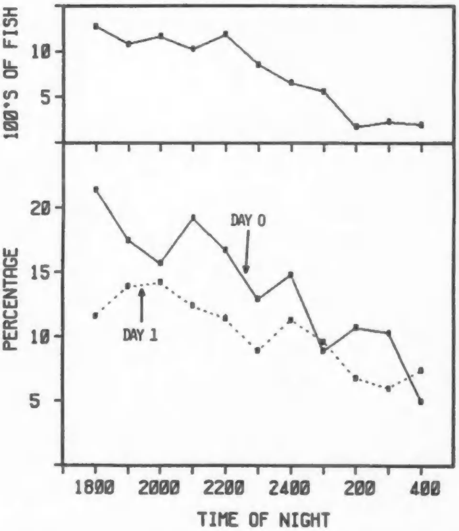

FIGURE 8.—The percentages of day-0 and day-1 female northern anchovies by time of night.

tivity, it is probable that the fishery undersamples the active spawners. In addition, a proportion of the commercial catches occur during the time of day when the females do not have hydrated eggs. The fishery data will therefore tend to underestimate the spawning incidence. The total sea survey data will also produce an underestimate as it includes samples taken throughout the night.

The combined fishery-sea survey data used in our analyses will therefore provide only an index of the daily spawning incidence. To evaluate the potential net bias of this index we calculated the percentage of females with maturity stages 5 + 6, in the combined fishery-sea survey data, and the percentage of females with day-1 postovulatory follicles, in the histological data. To make the data comparable we used the period 1977-84 and the months February-April. The percentage of females with maturity stages 5 + 6 and the percentage of females with day-1 postovulatory follicles was 10.9 and 11.5%. Use of the maturity stage data will therefore slightly underestimate the daily spawning incidence (i.e., 10.9/11.5 = 0.948).

Size Dependent Batch Fecundity

Annual fecundity in the northern anchovy is dependent upon the batch fecundity and the number of spawnings per year. Batch fecundity is size dependent and the best average estimate over six seasons (Hunter et al. 1985) is given below. Note that Hunter et al. found significant variation (ANOVA) among years.

$$\text{batch fecundity} = -1{,}104 + 614\ (\text{WT})$$

where WT = female wet weight, minus ovaries, in grams. During the spawning season ovary free weight of northern anchovy is equal to 95% of the total wet weight (Hunter and Leong 1981). Batch fecundity, with the above relationships, for a typical 1-yr-old (12 g) and a typical 4-yr-old (24 g) are 5,896 eggs and 12,895 eggs. On a per unit weight basis the 24 g fish would produce only 9.4% more eggs than the 12 g fish. Age-dependent variations in batch fecundity are therefore of only minor significance in the relationship between spawning biomass and annual fecundity. There is the possibility that batch fecundity could vary over the spawning season, and since we have shown an age-dependent seasonality in the spawning incidence of northern anchovy, this could potentially contribute to age-dependent differences in annual fecundity. Hunter and Leong (1981), however, found average batch fecundity to be essentially the same in samples taken in January-February and in March-April.

Size-Dependent Histology Classes

Hunter and Macewicz (1980) found no relationship between size and the percentage of mature female northern anchovy with day-1 postovulatory follicles. Later work by Picquelle and Hewitt (1984) showed that weight and spawning incidence were highly correlated in the northern portion of the central stocks range. They stated that this implied that the larger females spawned more frequently or that the smaller females had a much shorter spawning season. We analyzed the larger histology data set now available and found that the percentages of females with hydrated oocytes or with day-1 postovulatory follicles, as well as the percentage of females with maturity stages 5 + 6, were dependent upon the size of the females (Fig. 9).

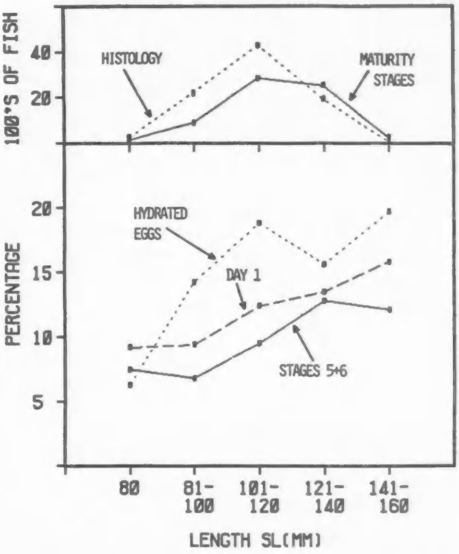

FIGURE 9.—The percentages of female northern anchovies with hydrated eggs, with maturity stages 5+6, and day-1 histological classes by size group.

Age-Dependent Spawning Incidence and Annual Fecundity

To assess age-dependent, annual fecundity in the central stock of northern anchovy we calculated the number of spawnings and the fecundity on a monthly basis for age groups 1, 2, 3, and 4+. Average monthly wet weight by age was taken from Mallicoate and Parrish (1981). The number of spawnings per month was calculated from the number of days per month and the index of daily spawning (i.e., the proportion of stages 5 + 6). Note that the bias due to the unknown sex problem discussed earlier would tend to cause an overestimation of the daily spawning incidence: particularly in females in their first spawning season. Also note that the index of daily spawning underestimates the spawning incidence by about 5%.

Our analysis shows that there are large, age-dependent variations in the proportions of female northern anchovy spawning as the spawning season progresses (Fig. 10). From July until January all age groups have a very low daily spawning index. Intensive spawning commences in February and all age groups have roughly the same spawning index (9-12%). In March the spawning index of age group 1 declines to about 2%; it increases slightly in April and declines to about 1% in May. In age group 2 the spawning index increases to 13% in March and then declines to about 2% by May. Age groups 3 and 4+ have peak spawning indices in March (25 and 27%), considerable spawning in April (10 and 17%) and lesser amounts in May (3 and 6%) and June (3 and 6%).

Older females have a much larger number of spawnings per spawning season than younger females (Table 3). In their first spawning season females have an average of 5.3 spawnings. In their second spawning season this rises to 11.9 and in their third and fourth plus seasons the number of spawnings rises to 19.2 and 23.5. The increase in the number of spawnings associated with increasing age appears to be primarily due to the increase in the length of the spawning season that occurs in older fish. The average number of spawnings per season for all females sampled was 15.1. This is less than the estimate that Hunter and Leong (1981) developed from the energetics of female northern anchovy (i.e., 20 spawnings per year). Their calculations indicated that mature female northern anchovy spawned on the average 15 times between February and September; their calculation of the number of spawnings from October to January (5) was estimated indirectly from the relative monthly larval abundance in 1953-60. Our estimate of the number of spawnings from February to September (14.3) is very close to the Hunter and Leong (1981) estimate which was based on a smaller histology data set. However, our estimate of the number of spawnings from October to January is only 0.8 and is much less than their indirect estimate based on the relative seasonal larval abundance for the 1953-60 period. The central stock of northern anchovy was at a much smaller population size in 1953-60 than it was in 1966-84 (MacCall 1980) and northern fish, with a seasonal spawning pattern similar to that occurring in the Monterey data, may have comprised a larger proportion of the anchovy population off California during the 1953-60 period than at present thus inflating Hunter and Leong's estimate for the October-January period.

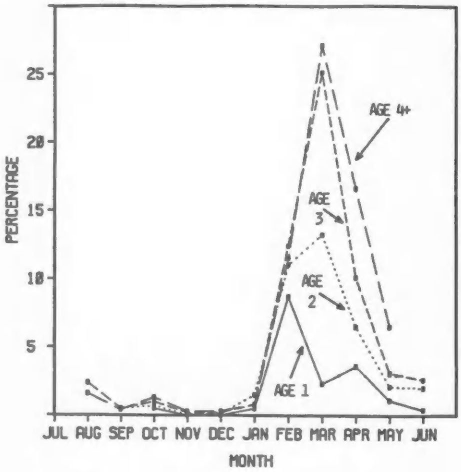

FIGURE 10.—The monthly percentages of female northern anchovies with maturity stages 5+6, by age group.

Our analysis indicates that annual fecundity in the central stock of northern anchovy is heavily age dependent; the average 4+ yr-old female produces nearly 10 times as many eggs as a 1-yr-old female (Table 3). Our calculations show that central stock, female anchovy produce 2,803, 6,550, 11,434, and 13,861 eggs/g of body weight per spawning season in their 1st, 2d, 3d, and 4th plus spawning seasons. Females 4 yr of age and older produce nearly 5 times as many eggs per unit of weight as 1-yr-olds.

DISCUSSION

Over the last decade it has become apparent that recruitment failure is the major threat to many of the world's largest fisheries. In addition, variation in recruitment is a significant causal factor in the interyear variation of the annual catches of many fisheries. Stocks of small pelagic fishes appear to

TABLE 3.—Proportion of maturity stages 5 + 6, number of spawnings and fecundity of female northern anchovies sampled in the Sea Survey Program (lat. 29.5°-34.5°N) and San Pedro fishery.

	July[1]	Aug.[1]	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	Total[2]	Eggs/g[3]
First spawning season														
Prop. 5 + 6	0.000	0.000	0.000	0.005	0.000	0.000	0.005	0.087	0.023	0.036	0.011	0.004		
Spawnings	0.000	0.000	0.000	0.155	0.000	0.000	0.155	2.436	0.713	1.080	0.341	0.120	5.3	
Wt. (g)	—	—	11.2	11.1	12.0	11.0	11.4	11.6	12.8	13.7	15.4	13.6		
No. eggs	0	0	0	832	0	0	860	13,793	4,536	7,438	2,687	819	32,514	2,803
Second spawning season														
Prop 5 + 6	0.002	0.000	0.005	0.007	0.001	0.001	0.015	0.110	0.132	0.065	0.021	0.020		
Spawnings	0.062	0.000	0.150	0.217	0.030	0.031	0.465	3.080	4.092	1.950	0.651	0.600	11.9	
Wt. (g)	15.5	15.5	17.4	16.8	17.2	16.3	16.2	15.6	16.5	17.7	18.3	17.5		
No. eggs	492	0	1,357	1,887	268	261	8,881	24,626	34,866	17,980	6,230	5,462	102,174	6,550
Third spawning season														
Prop. 5 + 6	0.022	0.024	0.005	0.010	0.002	0.002	0.008	0.124	0.251	0.101	0.031	0.026		
Spawnings	0.682	0.744	0.150	0.310	0.060	0.062	0.248	3.472	7.781	3.030	0.961	0.780	19.2	
Wt. (g)	18.3	18.3	19.1	19.3	19.2	19.3	19.1	18.0	20.7	22.2	20.9	22.7		
No. eggs	6,527	7,120	1,506	3,148	606	630	2,489	33,836	85,360	35,891	10,655	9,467	205,819	11,434
Fourth-plus spawning seasons														
Prop. 5 + 6	0.021	0.016	0.004	0.013	0.003	0.003	0.008	0.115	0.271	0.166	0.065	0.056		
Spawnings	0.651	0.496	0.120	0.403	0.090	0.093	0.248	3.220	8.401	4.980	2.015	1.680	23.5	
Wt. (g)	20.1	20.1	20.9	21.8	22.3	22.2	23.6	23.3	26.6	26.5	25.7	25.7		
No. eggs	6,914	5,268	1,330	4,680	1,071	1,102	2,952	37,390	110,293	67,123	26,454	18,136	322,957	13,861
All spawning seasons combined														
Prop. 5 + 6	0.017	0.021	0.008	0.011	0.002	0.002	0.010	0.107	0.151	0.094	0.044	0.012		
Spawnings	0.527	0.651	0.240	0.341	0.060	0.062	0.310	2.996	4.681	2.820	1.364	0.360	15.1	

[1] Missing data estimated from adjacent months.
[2] Includes 5% correction for spawning incidence bias.
[3] Total eggs/February weight.

be particularly susceptible to collapse; however, perturbations of recruitment is a potential threat to any fishery in which one or two year classes comprise the bulk of the landings. The stock-recruitment approach to understanding or predicting recruitment has fallen into disfavor, at least in the small pelagic fishes, because stock size has not proven to be a good predictor of recruitment. In its pure form (Beverton and Holt 1957; Cushing 1971; Ricker 1975) the stock-recruitment concept is based on two factors: 1) Parent stock size is a measure of the reproductive potential of the stock, and 2) there are compensatory mechanisms which reduce the number of recruits per spawner as the size of the parent stock increases. This compensation occurs through some mix of reduced fecundity of the parent stock, reduced growth of the recruiting cohort and increased mortality of the recruiting cohort. Recruitment variations are usually attributed to changes in environmental conditions, usually unknown, and the causal mechanisms, also usually unknown, are thought to occur during the early life history stages. The present emphasis of recruitment research is on the growth and mortality of the early life history stages. Potential variations of stock fecundity as a factor in recruitment variations has largely been ignored.

There are now 6 years of egg production estimates available for the central stock of northern anchovy (Bindman 1985). The mean spawning incidence for these years is 0.124 and the spawning incidence varied from 0.094 in the El Niño year of 1983 to 0.160 in 1984. This implies that the central stock produced 70% more eggs, per unit of spawning biomass, in 1984 than in 1983. Santander (1980) showed that the Peruvian anchoveta had both reduced spawning and an alteration of the seasonality of spawning during the 1972 El Niño. The results presented here, which show that fecundity is strongly age dependent, suggest that the reduction in age composition caused by heavy exploitation will greatly reduce the average fecundity per unit of biomass and also result in a reduction in the length of the spawning season. It appears that interyear variations in the age composition of a stock or in environmental factors associated with energy reserves or egg production are likely to alter greatly a stock's reproductive potential. If this is the case in other species which have multiple spawning, much of the variance in the stock-recruitment relationships of these fishes may be due to the fact that spawning biomass is a poor index of the reproductive potential of the stock.

To date information concerning age-specific reproductive potential has not been available for multiple spawning fishes because of the difficulty of determining the number of spawnings per year. The pioneering work by Hunter and Goldberg (1980) and later studies based on this work clearly demonstrate that, at least for many clupeids, the spawning incidence or spawning frequency can be determined with properly designed histological studies. Unfortunately a research program designed to determine age-specific reproductive potential would be very expensive as it would require a field sampling progam extending over the whole spawning season, in many cases the entire year; and it would require histological analysis and aging of a large number of females, both quite labor intensive.

It appears that the only way it may be possible to determine age-specific reproductive potential for many fishes is to use the approach developed here which combines two methodologies: histological assessment of ovaries because it unambiguously and accurately measure spawning rate and a traditional fishery sampling program which utilizes an inexpensive rapid index of reproductive condition, such as the maturity stage system or a gonado-somatic index, in which thousands of specimens can be processed. Whichever anatomical grading system is used, its principal purpose would be to determine the percentage of hydrated females. Most of the maturity stages (i.e., 1-4, 7) in the system used for northern anchovy are only of value in describing the seasonality of spawning. The only stages (i.e., 5 and 6) which can be used to determine the number of spawnings are those in which the eggs are hydrated, and they can be directly used as an index in northern anchovy because it is known that the duration of hydrated eggs in the ovary is <24 h. The traditional fishery sampling program may, as in the case for northern anchovy, already be available. If this is the case the principal work will be to calibrate properly the maturity stage or gonado-somatic index with the histological analysis. For this approach to work the fishery must, of course, take hydrated females.

CONCLUSIONS

It is important for those managing fisheries which are susceptible to recruitment overfishing to realize that the alteration in the age structure of a stock that occurs under heavy exploitation may have greater effects on the total fecundity and seasonality of spawning than previously recognized. Management strategies which decrease the exploitation of older, more fecund females could increase yields and also provide increased protection against recruitment overfishing. In northern anchovy there is the additional factor that the sex ratio in the fishery is age dependent (i.e., the female:male ratio for 1-yr-old anchovy in the San Pedro fishery is 0.83:1, whereas that for 4+ yr-olds is 2.01:1). When this factor is multiplied by the difference in the fecundity of the two age groups, it is apparent that the catch of a ton of 4+ yr-old northern anchovy reduces the reproductive potential of the stock 7.3 times as much as the catch of a ton of 1-yr-old fish.

ACKNOWLEDGMENTS

We gratefully acknowledge John Hunter and Beverly Macewicz for allowing us to use their extensive data on the histology of the ovaries of northern anchovy and Carol Kimbrell for providing us with the computer files. John Hunter also provided considerable input to the development of the work and edited the manuscript. We would also like to thank Eric Knaggs, Eugene Fleming, and John Sunada for providing us with the anchovy fishery data and Kenneth Mais for providing the sea survey anchovy data.

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SOME STATISTICAL TECHNIQUES FOR ESTIMATING ABUNDANCE INDICES FROM TRAWL SURVEYS

MICHAEL PENNINGTON[1]

ABSTRACT

Methods are presented for estimating an index of relative abundance from trawl survey catch per tow data. The estimated variance of the index takes into account the within survey variability in catch and possible yearly changes in catchability. Applying the techniques to a series of surveys for yellowtail flounder, *Limanda ferruginea*, off the northeast coast of the United States yields an abundance index with a variance which is 40% lower than the variance of the original survey index for the current value and 57% lower for values not near the ends of the survey series.

The average number of fish caught per tow during a trawl survey is often used as an index of a species's relative abundance (Grosslein 1969; Clark 1979). Catch per tow data are usually quite variable because of the heterogeneous distribution of many fish stocks (Byrne et al. 1981). A further source of variability for survey indices of abundance is that the catchability of a particular species with respect to the survey trawl may change from year to year (Byrne et al. 1981; Collie and Sissenwine 1983). As a result, the observed time series of abundance indices reflects changes in the population, within survey sampling variability, and varying catchability over time.

This paper uses various statistical methods to construct from the catch per tow data an index of abundance which more closely tracks the population than does the original (average catch per tow) series. Specifically, since the distribution of catch per tow data is often highly skewed and contains a proportion of zeros, estimates of the mean catch per tow for each survey are made based on the Δ-distribution (Aitchison and Brown 1957). Next, time series techniques are used to estimate the component of the series generated by the actual changes in the population.

The methods are applied to data for yellowtail flounder, *Limanda ferruginea*, from a series of groundfish trawl surveys conducted off the northeast coast of the United States as part of the National Marine Fisheries Service's MARMAP program. The resulting index of abundance is substantially more precise than the original index.

STATISTICAL METHODS

Sources of Variability

Let y_t denote the observed average catch per tow for the survey conducted in year t and $z_t' = E[y_t]$, the expected value of y_t. Since a species catchability may change from year to year with respect to the survey trawl, let $z = E[z'|p]$ denote the expected value of z' given a population level p. Then

$$y_t = z_t + e_t.$$

The error term, e_t, can be expressed as

$$e_t = (y_t - z_t') + (z_t' - z_t),$$

where the first error component is due to the within survey variability and the second is due to changes in catchability.

In order to construct an index of abundance, it is necessary to assume a functional relationship between z_t and p_t. A reasonable assumption made in practice (and in this paper) is that

$$z_t = ap_t.$$

If the relationship is not linear, then the unadjusted catch per tow index will be a biased measure of relative abundance.

Estimating the Mean Catch per Tow

The distribution of marine survey data often can be described by what is called a Δ-distribution (Aitchison and Brown 1957). That is, the data contain

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[1] Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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a proportion of zeros and the nonzero values are distributed lognormally. The minimum variance unbiased estimates of the mean, c, and its variance, var(c), for the Δ-distribution are given by (Pennington 1983),

$$c = \begin{cases} \dfrac{m}{n} \exp(\bar{y})\, G_m(s^2/2), & m > 1, \\[2ex] \dfrac{x_1}{n}, & m = 1, \\[2ex] 0, & m = 0, \end{cases} \tag{1}$$

and

$$\operatorname{var}(c) = \begin{cases} \dfrac{m}{n} \exp(2\bar{y}) \left[\dfrac{m}{n} G_m^2(s^2/2) - \left(\dfrac{m-1}{n-1} \right) \right. \\[2ex] \quad \left. \times\, G_m\left(\dfrac{m-2}{m-1} s^2 \right) \right], & m > 1, \\[2ex] \left(\dfrac{x_1}{n} \right)^2, & m = 1, \\[2ex] 0, & m = 0, \end{cases} \tag{2}$$

where n is the number of tows, m is the number of nonzero values, $\bar{y}$ and s^2 are the sample mean and variance respectively of the nonzero $\log_e$ values, x_1 is the single (untransformed) nonzero value when $m = 1$, and

$$G_m(x) = 1 + \frac{m-1}{m} x + \sum_{j=2}^{\infty} \frac{(m-1)^{2j-1} x^j}{m^j (m+1)(m+3)\ldots(m+2j-3)\, j!}.$$

The series defining $G_m(x)$ is a function of x [e.g., $x = s^2/2$ in Equation (1)] and m which is easily evaluated for particular values of x and m using a computer.

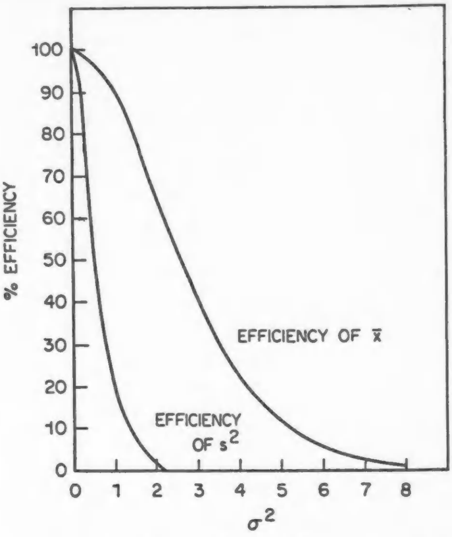

FIGURE 1.—The efficiency of $\bar{x}$ and s^2 (the sample mean and variance, respectively) for the Δ-distribution with 50% zeros.

Figure 1, which is an extension of a graph in Aitchison and Brown (1957, p. 98), shows the large sample efficiency of the ordinary sample statistics as compared with their most efficient estimates for the Δ-distribution with 50% zeros. Estimates of σ^2, the variance of the nonzero $\log_e$ values, are often between 1 and 2 for trawl surveys. Thus (Fig. 1) the sample mean is a fairly efficient estimator of the mean for trawl surveys, but the sample variance is highly inefficient. Though for larger values of σ^2, which, for example, are common for egg surveys (Pennington and Berrien 1984), the sample mean is also very inefficient. It does not follow that the variance of c is necessarily small, but it is smaller, and as σ^2 increases, much smaller than the variance of the sample mean. However, it should be noted that if the sample variance is used to estimate the variance of the sample mean for moderate sample sizes because of the inefficiency of the sample variance, the estimated variance of c will often be greater than the estimated variance of the sample mean.

Estimating the Index of Abundance

As an index of abundance, the series of yearly catch per tow estimates, y_t, (based, e.g., on the Δ-distribution theory if appropriate) has two drawbacks. First, its estimated variance when derived from the within survey variance can be an underestimate since catchability may vary from year to year. The second and more serious deficiency is that the index for a particular year is based only on that year's survey which disregards relevant information contained in the surveys for other years.

One method to construct an abundance index based on the entire survey series is briefly as follows (more details can be found in Pennington (1985)).

Suppose the population (or z_t) can be represented by the autoregressive integrated moving average process (Box and Jenkins 1976, Chap. 4)

$$\Phi(B)\, z_t = \theta(B)\, a_t.$$

where the a_t's are independently identically distributed (*iid*) and normally distributed (*N*) with mean zero and variance σ_a^2 [*iid* $N(0, \sigma_a^2)$]. If $y_t = z_t + e_t$, and the e_t's are assumed *iid* $N(0, \sigma_e^2)$, then y_t will follow the model

$$\Phi(B)\, y_t = \eta(B)\, c_t, \qquad (3)$$

where the c_t's are *iid* $N(0, \sigma_c^2)$. Now if model (3) and the ratio σ_e^2/σ_c^2 are known, then the maximum likelihood estimate of z_t is given by

$$\hat{z}_t = y_t - \frac{\sigma_e^2}{\sigma_c^2}(\hat{c}_t - \pi_1\, \hat{c}_{t+1} - \pi_2\, \hat{c}_{t+2} - ,\ldots, - \pi_{T-t}\, \hat{c}_T), \qquad (4)$$

where T denotes the last year of the series, the $\hat{c}_t$'s are the estimated residuals generated by model (3), and the π values are calculated using the identity

$$\Phi(B) = (1 - \pi_1 B - \pi_2 B^2 - \ldots)\, \eta(B). \qquad (5)$$

The variance of $\hat{z}_t$ is given approximately by

$$\mathrm{var}(\hat{z}_t) \doteq \sigma_e^2 \left[1 - (\pi_0^2 + \pi_1^2 + \ldots + \pi_{T-t}^2)\frac{\sigma_e^2}{\sigma_c^2}\right], \qquad (6)$$

where $\pi_0 = 1$.

The model for y_t [Equation (3)] is usually obtained in practice by fitting a model to the observed series using procedures described in Box and Jenkins (1976). If catchability is constant over time, the within survey sampling variance provides an estimate of $\sigma_e{}^2$. But if catchability varies, another approach is necessary.

Toward this end, consider the expression

$$z_t = z_{t-1}\, e^{a_t}$$

or

$$(1 - B) \ln z_t = a_t. \qquad (7)$$

Suppose the factors causing the change in population from year $t - 1$ to year t (such as recruitment, fishing mortality, natural mortality, and migrations) produce a_t's which are approximately *iid* $N(0, \sigma_a^2)$. If the measurement errors are multiplicative, then

$$\ln y_t = \ln z_t + e_t. \qquad (8)$$

Assuming the e_t's are *iid* $N(0, \sigma_e^2)$ and independent of the a_t's, then it follows as above that y_t can be represented by the model

$$(1 - B) \ln y_t = (1 - \theta B)\, c_t. \qquad (9)$$

where the c_t's are *iid* $N(0, \sigma_c^2)$

For model (9) [generated by Equations (7) and (8)]

$$\theta = \sigma_e^2/\sigma_c^2$$

and

$$(1 - \theta)^2 = \sigma_a^2/\sigma_c^2. \qquad (10)$$

Therefore, assuming the above approximations to the population dynamics, fitting model (9) to the observed survey series provides an estimate, $\hat{\theta}$, of σ_e^2/σ_c^2 and an estimate of σ_c^2. The π-weights for the model are from Equation (5) given by

$$\pi_i = (1 - \hat{\theta})\, \hat{\theta}^{i-1}, \qquad i \geqslant 1. \qquad (11)$$

It may be noted that if model (9) is valid and catchability is constant over time then the estimate of σ_e^2 given by $\hat{\theta}\, \hat{\sigma}_c^2$ [from Equation (10)] would approximately equal the estimate of σ_e^2 based on the within survey sampling variance.

AN APPLICATION

The Northeast Fisheries Center conducts an extensive groundfish trawl survey as part of its MARMAP program two times a year: in the fall since 1963 and in the spring since 1968 (Grosslein 1969). The survey region is divided into sampling strata based on geographic boundaries and depth contours (Fig. 2). For each survey, trawl stations are chosen randomly within each stratum. One of the objectives of the surveys is to provide indices of abundance for the many species of commercial value in the region.

Yellowtail flounder is an important New England fishery resource whose population has fluctuated considerably over the survey period (Clark et al. 1984). Commercial catch statistics exist for yellowtail flounder, but age data suitable for a VPA (Virtual Population Analysis) are unavailable. Major

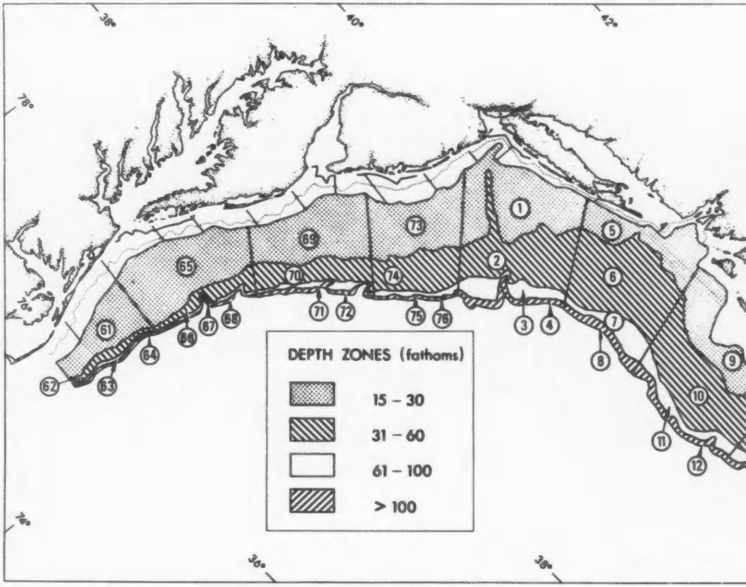
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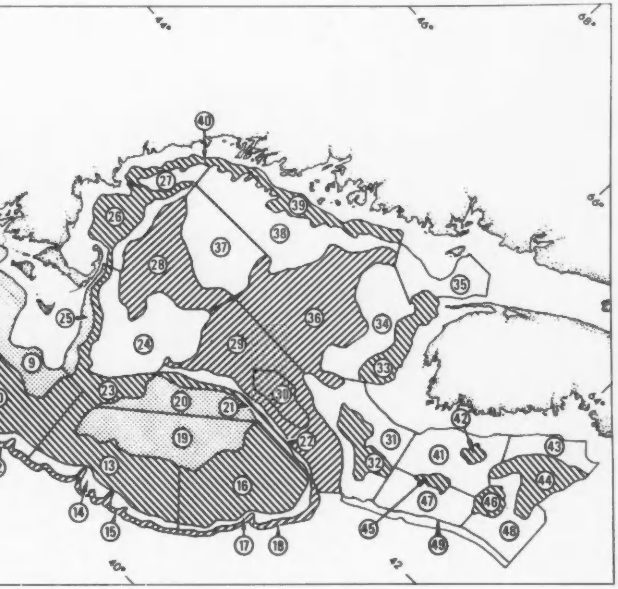
FIGURE 2.—The National Marine Fisheries Service'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Service's MARMAP survey strata.

yellowtail flounder fisheries are off southern New England (strata 5, 6, 8, 9) and on Georges Bank (strata 13-21). The two stocks are fairly distinct but with some intermixing (Clark et al. 1984).

The nonzero catch per tow survey data for yellowtail flounder are approximately lognormally distributed within a stratum. Therefore, the estimators based on the Δ-distribution [Equations (1) and (2)] were used to estimate the mean catch per tow and its variance in each stratum. The regional estimates for southern New England and Georges Bank were then calculated in the usual manner for each survey (see, e.g., Pennington and Brown 1981).

Model (9) was fit to each series (spring 1968-84 and fall 1963-84 in both regions) and the model's adequacy checked (Box and Jenkins 1976, Chap. 8). Table 1 contains summary statistics and parameter estimates for the four series. Since the series are relatively short, the averages of the areal and seasonal estimates are used as the final estimates of θ and σ_c^2 (last line in Table 1).

TABLE 1.—Summary statistics and parameter estimates for the yellowtail flounder survey series. The first three sample autocorrelations (r_1, r_2, and r_3) are for the first differenced logged series.

Survey	No. of years	r_1	r_2	r_3	$\hat{\theta}$	SE($\hat{\theta}$)	$\hat{\sigma}_c^2$
Southern New England							
Spring	17	−0.23	0.12	−0.18	0.21	0.28	0.57
Fall	22	−0.26	0.07	−0.31	0.40	0.22	0.71
Georges Bank							
Spring	17	−0.32	0.00	−0.09	0.61	0.23	0.36
Fall	22	−0.30	−0.06	0.18	0.36	0.23	0.33
Average		−0.28	0.03	−0.10	0.40	[1]0.12	0.50

[1] Assuming the estimates of θ are independent.

Abundance indices for the two regions and seasons were calculated by applying to each series Equation (4) with $\hat{\theta} = 0.4$, the π-weights given by Equation (11), and the $\hat{c}_t$'s (for each series) generated by model (9). An estimate of σ_e^2 equal to 0.20 and of σ_a^2 equal to 0.18 were obtained from Equation (10). The estimated variance of the index equals, from Equation (6), 0.12 for the current value and declines to 0.09 for values not near the series' end points. This compares with a variance of 0.20 (= $\hat{\sigma}_e^2$) for the original index. Figures 3 (log scale) and 4 (linear scale) show plots of the estimated index and the observed catch per tow series for the fall surveys off southern New England.

DISCUSSION

The major advantage of estimating an index of abundance from the entire survey series is that it can produce an index with a variance considerably smaller than the variance of the observed series. But the application also demonstrates that estimates of the accuracy of an index based only on the within survey sampling variance can be misleading. For example, the 1972 survey value for yellowtail flounder off southern New England is considered an anom-

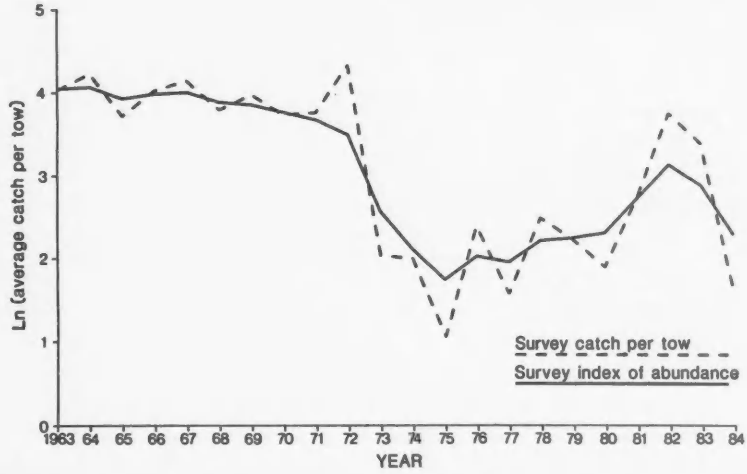

FIGURE 3.—Logged average catch per tow and the estimated index of abundance for southern New England yellowtail flounder.

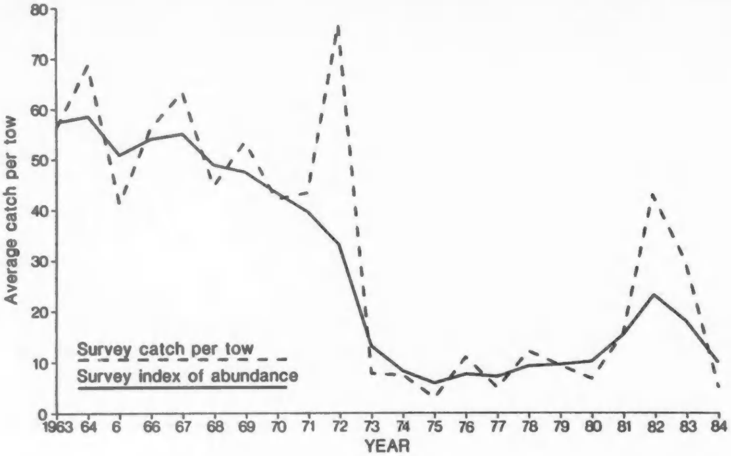

FIGURE 4.—Average catch per tow and the estimated index of abundance for southern New England yellowtail flounder.

aly (Collie and Sissenwine 1983). It does appear anomalous if comparisons are made using 0.11, the estimated variance based on the within survey variance, but not if the estimate of 0.20 (= $\hat{\sigma}_{\epsilon}^{2}$) is considered (Fig. 3).

Assessing the accuracy of an index of abundance for marine stocks is difficult since the true levels are never known with certainty. But they can be compared with other indicators of abundance. The methods were applied to the haddock stock on Georges Bank (Pennington 1985) for which a VPA exists. It was found that model (7) adequately describes the dynamics of the VPA series, and the survey series follows model (9). The resulting index of abundance is quite similar to the VPA estimates.

Collie and Sissenwine (1983) give a method for estimating the relative abundance of a fish stock using survey data and commercial catch statistics. They observe that their method produces estimates which compare favorably with VPA estimates. Figure 5 shows plots of Collie and Sissenwine's estimate of the relative abundance of southern New England yellowtail flounder and the index based only on the survey data.

Finally, it should be noted that the purpose of the modeling stage in the estimation procedure is not necessarily to develop a realistic model for the population, but to describe the important stochastic properties of the series. As the observed series becomes longer, more precise estimates can be made. For shorter series, given the large variability inherent in marine trawl surveys, a preliminary estimate of between 0.3 and 0.4 for the smoothing parameter θ appears to be an appropriate initial value to use for estimating an abundance index until more information becomes available.

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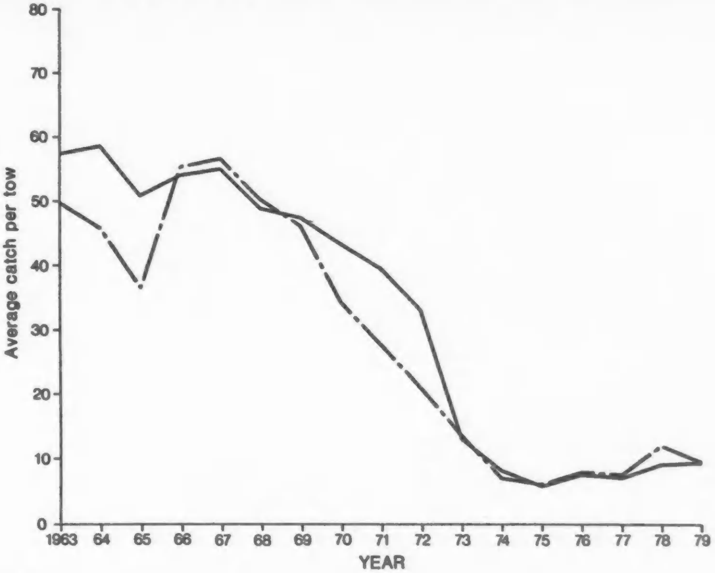

FIGURE 5.—Survey index of abundance (solid line) and Collie and Sissenwine's index (broken line) for southern New England yellowtail flounder.

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RATES OF INCREASE IN DOLPHIN POPULATION SIZE

Stephen B. Reilly and Jay Barlow[1]

ABSTRACT

Annual finite rates of increase in dolphin population size were estimated to vary up to a maximum of 1.09, using simulation, based on ranges in vital rates. Vital rate ranges were defined from values reported in the literature where possible, otherwise by making assumptions about biological or logical limits. Given information on current values, or limits, of one or more vital rate, one can use the figures presented to determine ranges of possible rates of increase in population size. The highest rates estimated here (up to 1.09) are probably unrealistic, because of the unlikely combinations of high fecundity and low mortality needed to achieve them.

Rates of increase in population size are important in determining management strategies for fish and wildlife subject to exploitation. A common management approach for setting incidental mortality or harvest quotas is to use a stock-production model (Schaeffer 1957; Allen 1976) with an assumed maximum rate of increase. For dolphins and other cetaceans, rates of increase have proven extremely difficult to measure directly. Nonetheless, estimates of this parameter are sometimes necessary, e.g., in setting incidental mortality quotas for dolphin populations involved in the eastern tropical Pacific purse seine fishery for yellowfin tuna (Smith 1983). In such situations, even a range, when rigorously defined, can contribute substantially to delineating the management options.

In this paper we define a range of reasonable values of rate of increase (hereafter also referred to as ROI) in dolphin population size, given what is known or can be inferred about their age-specific survival and fecundity distributions, or "vital rates". We estimate rates of increase using population projection matrices for various parameter combinations. We also suggest how the resulting ranges in ROI can be further narrowed, given specific information for an individual population.

There are many slightly different definitions for rate of increase, but all share the commonsense notion of change in population size over time. Caughley (1977) reiterated the distinction between exponential and finite rates: finite rates, here symbolized λ, are related to exponential rates, here symbolized r, by the simple conversion $\lambda = e^r$. (We use the term "finite rates of increase" for λ following Birch 1948.) Further, within exponential rates Caughley distinguished among "intrinsic" (r_m), "survival-fecundity" (r_s) and "observed" ($\bar{r}$), rates.

In this paper we compute a series of r_s values, resulting from ranges of survival-fecundity distributions. The highest value of r_s resulting from the range of vital rates considered is our best estimate of dolphin r_m, or "r-max".

We define the ranges in vital rates based on the literature for dolphins where possible. Otherwise, we rely on information for other large mammals and what appear to be logical or biological limits.

There are two previous studies of a similar nature for delphinids. As part of a general review of life history analysis of large mammals, Goodman (1981) examined the relationships among rate of increase, juvenile and adult survival rates. He looked at single values for calving interval and age at first reproduction across ranges of survival rates. We take a broader look at these relationships, examining ranges for all four parameters.

Polacheck (1984) examined interparameter relationships for eastern tropical Pacific (ETP) dolphins, *Stenella* spp., given specific vital rate estimates available as of 1981, showing the values were not consistent with a positive population growth rate. Since then, revised estimates have become available for some relevant parameters, and this specific case has been reanalyzed, with similar general conclusions.

The only reported dolphin rates of increase are for *Stenella coeruleoalba*. For the year 1974, Kasuya (1976) estimated a rate of 0.024 for the population off Japan. This value was computed in a complex manner, based on an observed fishing mortality, assumed natural mortality, and estimated popula-

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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tion size, calving interval and sex ratio. Assuming that calving interval was density dependent, Kasuya (1976) estimated a maximum annual rate of increase of 0.044 for this population of *S. coeruleoalba.*

METHODS

The Model

Population growth rates are estimated here using the familiar Leslie matrix model (Leslie 1945). A simplified parameterization is used for which survival rates and fecundities remain constant over many age classes. Four parameters are required: 1) calving interval for reproductively mature females, 2) average age at first birth for females, 3) annual adult (noncalf) survival rate, and 4) annual calf survival rate. This degree of detail corresponds to the practical limitations in collecting data on wild dolphin stocks.

The model is constructed with the assumption that age class 1 corresponds to newly born calves (i.e., censuses occur immediately after the calving season). In fact, the model is not dependent on discrete calving seasons, but this assumption helps in conceptualizing some elements of the model. The fecundities (elements of the first row of the Leslie matrix) represent the number of female calves born in one year per female of a given age class in the previous year. Fecundities for mature age classes are estimated as the annual pregnancy rate (the inverse of calving interval) multiplied by the adult survival rate (the probability that a [pregnant] female will survive to the calving season) multiplied by 0.5 (the fraction of female offspring). The annual pregnancy rate is estimated as the percent of sexually mature females which are pregnant, divided by the gestation period (in years).

The choice of only two different survival rates for all life stages was made because of data limitations for dolphins. Perhaps a more biologically reasonable assumption would be that dolphins have a U-shaped mortality curve which is characteristic of mammals in general (Spinage 1972; Caughley 1977; Siler 1979; Smith and Polacheck 1981). Barlow[2] incorporated this typical mammalian survivorship curve in models of growth for spotted dolphins, *Stenella attenuata.* Our choice of a separate survival rate for calves was based on the common observation of higher mortality in juvenile mammals (Caughley 1977; Siler 1979). For convenience, juvenile mortality factors are compressed into the first year's survival rates. This simplification is justified because population growth rates do not depend on the age at which juvenile mortality actually occurs. We recognize that juvenile mortality factors probably extend past the first year of life, but insufficient data exist to justify including this in our model. Higher mortality in old age was not incorporated in our model, but maximum age was limited to 50 yr. The survival rate at age 50 was thus zero.

We calculate population growth rates for a range of the four vital rate parameters mentioned above. Finite population growth rates, λ, that are associated with these parameter values were calculated by solving Lotka's characteristic equation, using Newton's method. The explicit form of Lotka's equation used is

$$1 = \sum_{x=1}^{50} \lambda^{-x} l_x m_x$$

where l_x is the survivorship from birth to age class x and m_x is the fecundity of age class x.

Below, we define the ranges used for the four population parameters and describe how they were selected.

Survival Rates

Ranges in Noncalf Survival Rates

Few estimates of adult survival rates for dolphins are available in the literature, primarily because adequate data are difficult to collect. Kasuya (1976) presented annual survival rate estimates of 0.925 and 0.882 for exploited populations of *Stenella attenuata* and *S. coeruleoalba*, respectively; however, his method (log-linear regression) is biased (Barlow 1982), and he did not adjust for the effect of population growth on age structure. A range of 0.85 to 0.97 was chosen for survival rates in this study. Values <0.85 do not allow population growth for the ranges of other parameters appropriate here, hence these values were not considered. Values higher than 0.97 result in more than 22% of the population being over 50 yr old. This is inconsistent with estimates of longevity for delphinids based on tooth layer counts [58 yr in *S. coeruleoalba* (Sacher 1980), 38 yr in *S. attenuata* (Hohn and Myrick[3])], hence values

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[2] Barlow, Jay. 1986. Biological limits on current growth rate of a spotted dolphin population (*Stenella attenuata*). Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[3] Hohn, A. A., and A. C. Myrick, Jr. 1986. Age distribution of the kill of spotted dolphins in the eastern tropical Pacific.

>0.97 are untenable as mean per-capita survival rates.

Ranges in Calf Survival Rate

Again little information is available on calf survival for dolphins. Kasuya (1976) estimated a juvenile survival rate that was higher than that of adults, based on a balance equation. His methods assume that populations are neither growing nor declining, and he did not show that this assumption was met. Also his juvenile period included all sexually immature age classes. The overwhelming body of evidence from terrestrial mammals is that very early juvenile mortality is higher than adult mortality (Spinage 1972; Caughley 1977; Siler 1979). Even human populations had a first year survival rate of <0.88 prior to modern antibiotics (Fruehling 1982, data for U.S. circa 1900). An upper limit on calf survival rates was generated by assuming a calf is absolutely dependent on its mother for 1 yr. A calf has the same risk of dying as an adult, plus the additional risk of dying of starvation if its mother dies before completing 1 yr of lactation. The upper limit on calf survival would thus equal the square of the adult survival rate. The lower limit on calf survival rates was chosen as 0.50, a value that seems typical of pinnipeds (Smith and Polacheck 1981) and long-lived terrestrial mammals (Spinage 1972).

Fecundity-Related Rates

Ranges in Calving Interval

Observed calving intervals for dolphins generally range from 2 to 4 yr (Perrin and Reilly 1984); consequently, we have used this range in our computations. Intervals reported for killer whales (which are also delphinids, but not "dolphins") are considerably longer, up to 8 yr (e.g., Jonsgård and Lyshoel 1970).

The literature includes reports of calving intervals <2 yr for dolphins. These reports do not appear to be valid. Reevaluation of data for three of these reports[4] indicates that sampling was biased toward pregnant females (Perrin and Reilly 1984), a result of what may be a general tendency for dolphins to segregate by age/sex groupings[5].

The remaining reports of calving intervals <2 yr are from very small sample sizes.[6] Gestation periods for dolphins are at minimum 10 mo, and intraspecific variation is small. Reported lactation periods range from 1 yr to over 2 yr (Perrin and Reilly 1984). Summing these two periods gives another indication that dolphin calving intervals are not likely to be <2 yr.

An exception to the 2-yr minimum calving interval would possibly be in a population experiencing very high calf mortality, causing premature cessation of lactation, and allowing females the opportunity to begin a new calving cycle (assuming there was no seasonality to breeding which could require a resting period before the next breeding season). To include consideration of this case we would need to devise an arbitrary function relating low calf survival to short calving intervals. The net result would again be low rates of increase. To avoid such complications we have simply used 2 yr as the minimum average calving interval.

Ranges in Age at First Birth

The available data suggest a range in age at attainment of sexual maturity of 6 to 12 yr for dolphins (Perrin and Reilly 1984). Early reports of Black Sea common dolphins, *Delphinus delphis*, attaining sexual maturity at an average of 3 yr (Kleinenberg 1956) are almost certainly due to faulty age determination[7]. Because of the recent findings for *S. attenuata* from the ETP (Myrick et al. 1986), we considered the ages at first birth up to 15 yr. In our formulation of the Leslie model, if females mature and first conceive at an average age of 10 yr, the first nonzero fecundity would be in age class 11 (Table 1).

TABLE 1.—Parameters used and values included in the computation of rates of increase in dolphin population size.

Parameter	Values
Calving interval	2 yr 3 yr 4 yr
Age at first birth	7 yr 9 yr 11 yr 13 yr 15 yr
Calf survival rate	0.50 0.52 0.54 . . . $(Sa)^2$
Noncalf survival rate (Sa)	0.850 0.855 0.860 0.865 . . . 0.970

Unpubl. manuscr. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[4] Three reported cases of dolphin calving intervals <2 yr, later found to be biased due to age and sex segregation, are Black Sea *Delphinus delphis* and *Tursiops truncatus* (Kleinenberg 1956) and Western Pacific *Stenella coeruleoalba* (Miyazaki and Nishiwaki 1978).

[5] Hohn, A. A., and M. D. Scott. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Fifth Biennial Conf. Biol. Mar. Mammals, Abstr., p. 47.

[6] Henderson, J. R., W. F. Perrin, and R. B. Miller. 1980. Rate of gross annual reproduction in dolphin populations (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, 1973-78. Southwest Fisheries Center, La Jolla, California, Admin. Rep. LJ-80-02, 51 p.

[7] Myrick, A. C. Jr., Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038, pers. commun. June 1984.

RESULTS

Figures 1 through 5 give finite rates of increase (displayed as $(\lambda - 1) \cdot 100$) for the above ranges of age at first birth, calving interval, and calf and noncalf survival. The lower left corner of each panel is blank because we did not consider cases where calf survival exceeded the square of noncalf survival, for the reason discussed in Methods.

The maximum finite rates of increase which would result from the parameter ranges included here are 1.08 to 1.09. Rates as low as 0.89, i.e., decrease of 11%/yr. also resulted from the parameter ranges used.

Within the ranges of parameters examined here, rate of increase is most sensitive to calving interval and noncalf survival rate, followed by age at first birth, and is relatively insensitive to changes in calf survival rate. This is an expected result following the reports by Eberhardt and Siniff (1977) and Goodman (1981). An increase in calving interval of 1 yr results in a decrease in ROI of about 0.02, holding other parameters constant. For example, the maximum ROI for a 9 yr age at first birth is about 1.07 with a 2 yr calving interval. This ROI drops to 1.05 with a 3 yr calving interval. A decrease of 0.01 in noncalf survival rate results in a 0.01 decrease in ROI, while a 0.10 decrease in calf survival rate decreases ROI by <0.01. Age at first birth appears to be nonlinearly related to ROI over the ranges examined here. An increase in this age from 7 to 9 yr results in a 0.02 decrease in ROI, while an increase

FIGURES 1-5.—Contours of percent rate of increase in dolphin population size $((\lambda - 1) \cdot 100)$, as a function

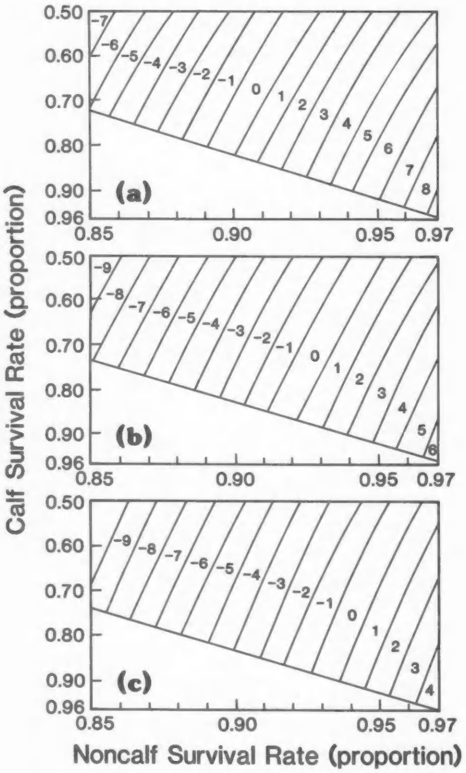

FIGURE 1.—First reproduction of dolphin age class 7 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

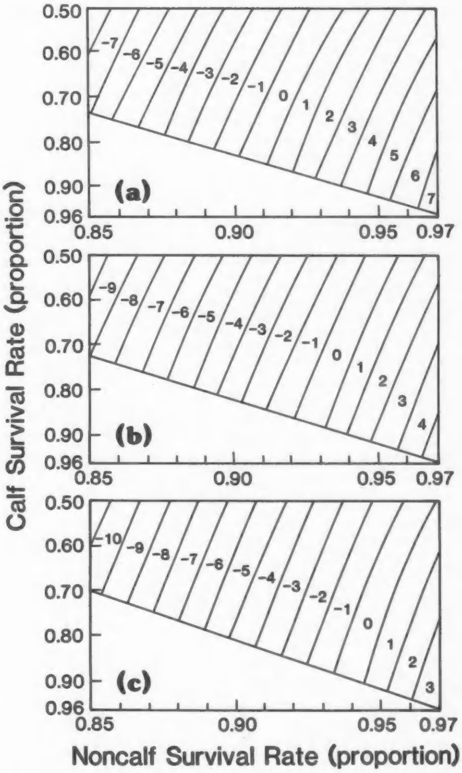

FIGURE 2.—First reproduction of dolphin age class 9 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

from 11 to 13 yr causes only a 0.01 decrease in ROI.

DISCUSSION

The ranges of rate of increase estimated here are potentially useful in bracketing possible ROIs for delphinids in general. For any particular population it should be possible to further narrow the range of likely values of ROI, given available estimates for vital rates. For example, *Tursiops truncatus* from the northeast coast of Florida reportedly attain sexual maturity at 12 yr on the average (Sergeant et al. 1973) and have a 12-mo gestation period (Essapian 1963), giving an estimated age at first birth of 13 yr. Knowledge of this single parameter can narrow consideration to Figure 4. Here the estimated range in ROI is up to a maximum of 1.05, for the extreme case of an average calving interval of 2 yr, and noncalf survival >0.96. Additional knowledge of, say, minimal calving interval for *Tursiops* could further narrow consideration to one of the three panels of Figure 4, and establish minimal survival rates for positive growth rates, or the maximum rate of increase possible, given the above constraints on age at first birth and calving interval.

We assume that the ranges defined here also encompass the limits within which vital rates for any one dolphin species might change in response to changes in population density. This obviously entails making simplistic assumptions about density dependence in vital rates, and therefore in rate of increase.

of calf and noncalf survival rates, for the following combinations of calving interval and age at first reproduction:

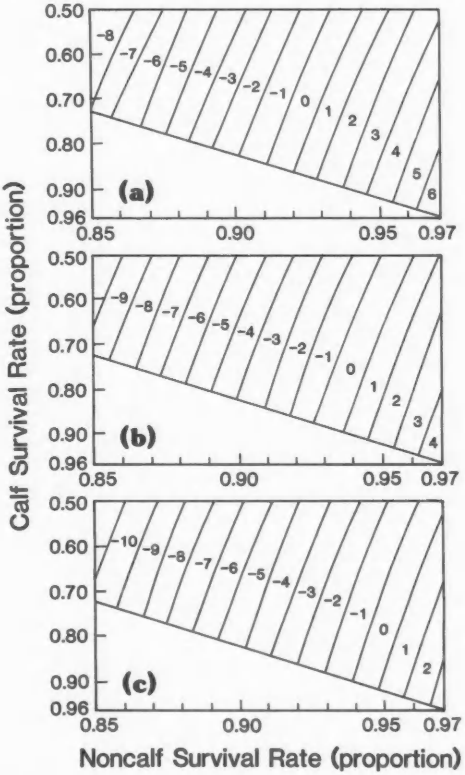

FIGURE 3.—First reproduction of dolphin age class 11 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

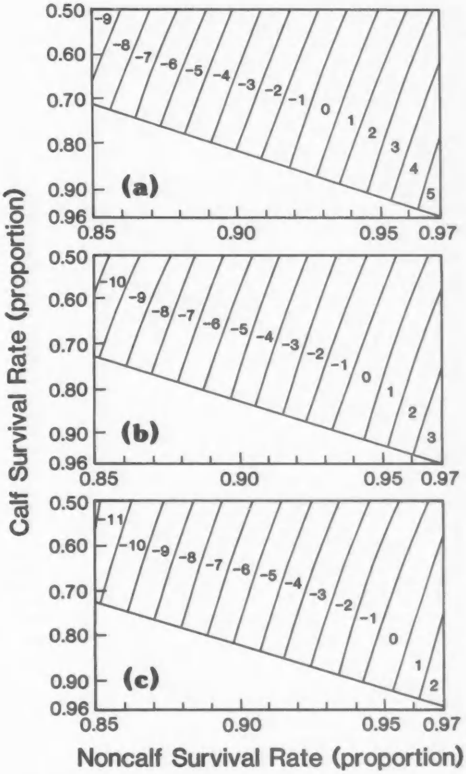

FIGURE 4.—First reproduction of dolphin age class 13 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

These assumptions are implicit in the concept of *r*-max.

There is no evidence that the highest rates of increase calculated here can be achieved by any real dolphin population. Trade offs may exist between survival and reproduction. Because of this, some of the parameter combinations examined here are probably unlikely, especially combinations of the extreme values, i.e., those producing the highest rates of increase.

Although our figures also present minimum values based on parameter combinations we used, we do not believe that these will be useful in setting lower bounds on finite rates of increase. Catastrophic events can always lead to rapid extirpation of a population. In fact, it is clear that dolphins (and other animals with similar life histories) can decrease in number much faster than they can increase.

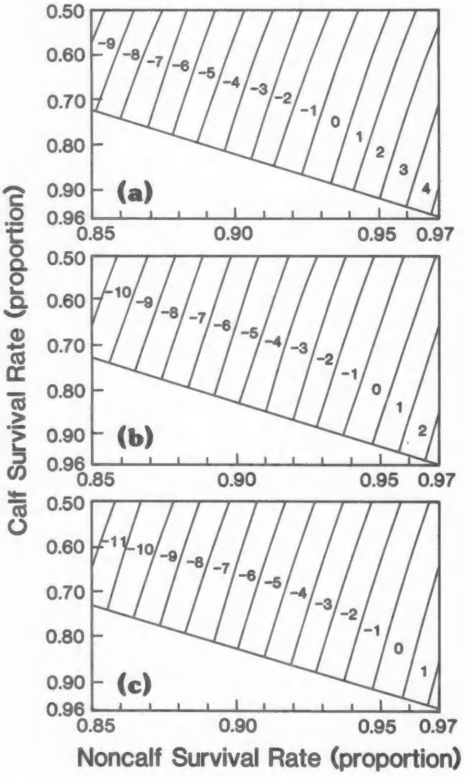

FIGURE 5.—First reproduction of dolphin age class 15 yr: a) 2-yr calving interval (upper panel); b) 3-yr calving interval (middle panel); c) 4-yr calving interval (lower panel).

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DISCRETE-TIME DIFFERENCE MODEL FOR SIMULATING INTERACTING FISH POPULATION DYNAMICS

C. ALLEN ATKINSON[1]

ABSTRACT

The dynamics of interacting fish populations are modeled using a coupled set of discrete-time difference equations. The basic equations describe predator-prey and competitive relationships analagous to the first-order expressions used in standard differential equation models. Population births and aging are represented using a modified Leslie matrix. A spatial representation is also incorporated and consists of a number of separate compartments, each containing interacting population groups which can be interchanged between compartments during a given time period. The potential applicability of the discrete-time formulation is demonstrated via a simulation of the multispecies fish populations within the California Current during the sardine population collapse of 1930-60.

Numerous mathematical models of interacting multispecies fish populations are found in the literature (Riffenburgh 1969; Saila and Parrish 1972; May et al. 1979; Steele 1979). Depending on the nature of a particular ecosystem and the desired resolution level for its components and processes, these models can become extremely complex (Parrish 1975; Anderson and Ursin 1977; Laevastu and Favorite 1978). The major limitation in practical fisheries applications is the lack of sufficient field data to adequately estimate many of the model parameters, particularly the population interaction terms in complex multispecies models (Goodall 1972).

The two objectives in the present multispecies model development are 1) to establish a general mathematical form applicable to a variety of practical fisheries problems and 2) to provide an efficient computational tool for simulating complex multispecies systems. The latter feature has implications for dealing with the problem of model parameter uncertainty via specialized Monte Carlo and nonlinear programming procedures as discussed by Atkinson (1985).

The proposed formulation consists of a unique set of discrete-time difference equations that describe first-order dynamic processes affecting some arbitrary number of interacting fish populations at one or more trophic levels. The discrete equations are particularly well suited for computer implementation. There are no requirements for sophisticated integration routines (e.g., Runge-Kutta, Adams-Moulton), and the equations have inherent numerical stability. Difference equations are also compatible with fisheries data sets (e.g., eggs and larvae surveys) which are usually sampled seasonally.

The essential biological processes represented in the model are spawning, growth, mortalities, age class structure, nonuniform spatial distributions, and migrations. Certain of these features, such as spawning, sexual maturation, and migrations, are often most conveniently described in a discrete form as assumed in the model. Seasonal time steps are natural increments for consideration as the values of appropriate model parameters can then be easily changed to relate seasonal fish behavior.

The mathematical details of the discrete-time difference model are developed below. The special problem of estimating model parameters in practical applications is also briefly discussed. The dynamics of the California Current fish populations are then modeled and simulation runs performed corresponding to the period of the sardine collapse in 1930-60. Comparisons are made between the simulation results and the actual (estimated) population responses.

DEVELOPMENT OF THE DISCRETE-TIME DIFFERENCE EQUATIONS

The dominant first-order ecological processes affecting fish populations are modeled by discrete-time difference equations. For convenience in the mathematical development, these processes are assumed to occur in the following sequence during a given time period: 1) individual growth and mortalities; 2) spatial redistributions of the surviving members; and 3) births and age class changes of the surviving,

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[1] System Science Applications, Inc., 121 Via Pasqual, Redondo Beach, CA 90277.

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redistributed populations. Consistent with the first-order nature of the formulas, certain simplifications are expected to be incorporated in the ecological representation including implicit modeling of lower trophic levels (e.g., phytoplankton and zooplankton) and functional groupings of less important species as competitors, predators, and prey.

Growth and Mortalities

First-order differential equations of the following general form are typically used to describe the growth and mortalities of a population P_i under competitive and predator-prey influences with itself and other populations:

$$\frac{d\,P_i}{d\,t} = (r_i - u_i P - v_i P + w_i P)P_i \tag{1}$$

where r_i = survival/growth parameter
P = population vector
$= (P_1, P_2, \ldots, P_i, \ldots, P_n)$
u_i = competition coefficient vector
$= (u_{i1}, u_{i2}, \ldots, u_{ii}, \ldots, u_{in})$
v_i = predation coefficient vector
w_i = prey coefficient vector.

The coefficient vectors u_i, v_i, and w_i contain appropriate zeros such that only the active interactions between populations are defined. (Note that vector multiplication is implied by the forms such as $u_i P$.) The competition terms correspond to the standard Gause model, while the predator-prey terms correspond to the simple Lotka-Volterra model (Pielou 1977). The population variables P_i can be expressed in units of either numbers of individuals or total biomass, with the coefficients defined accordingly.

Assuming a small time step (Δt) relative to the characteristic time of the system ($1/r$), a discrete-time approximation is found directly by integrating Equation (1) to give

$$P_i(\Delta t) = e^{r_i \Delta t} \cdot e^{-u_i P \Delta t} \cdot e^{-v_i P \Delta t} \cdot e^{w_i P \Delta t} \cdot P_i(0) \tag{2}$$

These exponential terms form the basis of the difference model. However, some modification and interpretation of terms is required in order to describe a general form appropriate over a range of population levels.

The most obvious inadequacy of Equation (2) is the positive exponential prey term, $e^{w_i P \Delta t}$, which gets increasingly larger as prey increases without ever reaching a saturation condition. A more appropriate form is the predator feeding model given by Ivlev (1961):

$$F = F_{\max}\,(1 - e^{-\zeta P}) \tag{3}$$

where F is the predator feeding ration and ζ is an associated prey coefficient, assuming that this form can also be used to describe the predator's growth/survival as a function of prey density.

The proposed difference equation for expressing population growth and mortalities during a Δt time step is

$$P_i(t + 1) = S_i\, e^{-\alpha_i P}\, e^{-\beta_i P}\, (1 - R_i\, e^{-\gamma_i P}) P_i(t) \tag{4}$$

where S_i = maximum survival/growth rate per time period
α_i = discrete form of competition coefficient vector
β_i = discrete form of predation coefficient vector
R_i = starvation mortality factor
γ_i = discrete form of prey coefficient vector.

The terms in this generalized form need further discussion and interpretation.

The maximum survival/growth rate factor, S, accounts for population births (if single age class), growth (if biomass units), and certain mortalities such as fishing, disease, and old age. It also accounts for predatory deaths caused by populations not explicitly included in the ecosystem model. It does not account for predation, competition, and prey availability effects associated with the modeled populations, which are explicitly stated by the other terms of Equation (4). Maximum survival/growth is defined under ideal conditions when competition and predation influences are negligible and there is an abundant supply of prey.

The α competition coefficient is the exponential equivalent to the Gause term in Equation (1) and represents a basic damping factor inhibiting population expansion. Self-competition generally relates to the essential environmental resources such as food supply and habitat space. Additional intrapopulation effects can come into play at the extreme ranges of population densities to complicate this interpretation, such as decreased fecundity caused by crowding (Parrish 1975) and decreased birth rates at very low densities (May 1973). Competition between population groups involves considerations of niche overlap relative to the common resources for which they compete (May 1973). Active competition interference effects may also be involved (Levine 1976; Vance 1978). Since my model deals only with first-order effects, the components of the coefficient vector α are defined as constants and assumed to be related to the dominant competitive mechanisms acting over the range of population densities expected in the simulation.

The β predation coefficient in Equation (4) corresponds to the Lotka-Volterra term in the differential equation and implies unlimited attack capacity per predator (May 1973). Relative values of these vector components reflect the comparative attack rates of the different predators in the model. The effective β coefficients perhaps should be reduced when there are relatively few predators compared with the size of population P_i because of saturated feeding. However, predation is probably a secondary factor under these conditions as competitive limitations will tend to dominate. Based on first-order arguments, constant β components are assumed to apply over a reasonable range of predator densities. Leslie and Grower (1960) make a similar assumption in the prey equation of their two-component predator-prey model. Their predator response equation, on the other hand, saturates at high relative prey levels as in the present model.

The prey form, represented in Equation (4), reflects Ivlev's form (Equation (3)) and implies some upper bound survival/growth rate under abundant prey conditions. The present form also incorporates a starvation mortality parameter, R, that describes a worst case condition without prey. This parameter would typically equal one unless the Δt time step is short or an alternative food source not explicitly included in the modeling is available to sustain the population.

Component magnitudes of the prey coefficient vector, γ, relate differences in the relative efficiency with which alternative prey are captured and utilized for predator growth and/or survival. At similar prey densities, a predator may utilize different capture methods and feed at higher or lower rates depending on the size and behavioral characteristics of a particular prey (Parsons and Takahashi 1973). Note, however, from the form of the exponential prey term in Equation (4), that any one sufficiently abundant prey population can satisfy the predator feeding requirement.

Finally, in comparing the present development with traditional fishery models, note that Equation (4) can be directly related to the single species recruitment models of Ricker (1958) and Beverton and Holt (1957) if the time step is defined as the maturation time between spawning and recruitment. Also, a comparable fishing term can be broken out of the survival/growth parameter as follows:

$$S = S_f S_0 \tag{5}$$

where S_f is the fishing survival rate and S_0 incorporates the remaining survival/growth effects. A corresponding fishing mortality rate, f, can be defined and related to fishing effort, E_f, as in the Beverton and Holt (1957) model:

$$f = \frac{-\ln S_f}{\Delta t} = \frac{\epsilon_f E_f}{A_f} \tag{6}$$

where ϵ_f is the fishing efficiency and A_f is the fishing area. The general compatability with traditional fishery models is stressed.

Spatial Redistributions

A simplified picture of fish stock migratory patterns during a typical life cycle is illustrated in Figure 1. Adult fish move from the feeding grounds to the spawning grounds and return; larval fish drift from the spawning to the nursery ground; and recruits join the adult stock on the feeding grounds. The seasonal timing of these events is quite regular as are the spatial regions to which the stock return during the cycle (Cushing 1975).

Large-scale spatial patterns will be represented in the model by a number of "boxes" or compartments, each with a defined size and each contain-

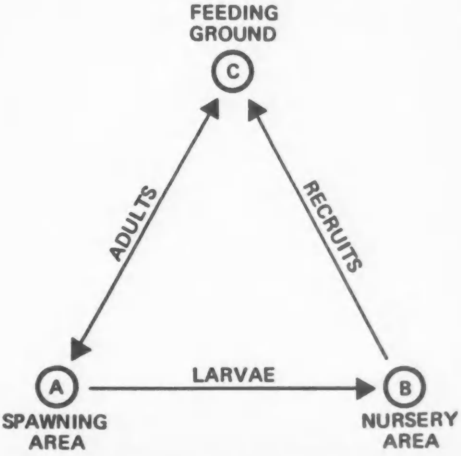


FIGURE 1.—Typical fish migratory pattern (from Cushing 1975).

ing segments of the various ecosystem populations. Population variables will now be uniquely assigned for each box and expressed in density units, such as numbers or kilograms per hectare. Spatial redistributions are assumed to occur during a given time period via migration, net drift, or turbulent dispersion. The resultant redistribution process is expressed by defining population transfers between boxes.

Spatial redistribution is applied to the surviving populations determined from Equation (4) and is described by

$$P_i^k(t+1,2) = \sum_{m=1}^{M} g_i^{mk} P_i^m(t+1,1) \qquad (7)$$

where

$P_i^k(t+1,2)$ = density of surviving population i in compartment k after spatial redistributions

$P_i^m(t+1,1)$ = density of surviving population i in compartment m before spatial redistributions

M = total number of spatial compartments

g_i^{mk} = population i transport coefficient for the exchange from compartment m to compartment k.

The g coefficient defines the population fraction involved in the exchange with an adjustment to account for the difference in area or volume between compartments. If no transit occurs between compartments, the value of the respective coefficient is zero.

Birth and Aging Processes

The larvae and juvenile age classes of fish populations have markedly different survival rates and behavioral characteristics than do adult populations. These differences have potentially important first-order ecological consequences and are, therefore, of concern in the present model development.

A modified version of the Leslie matrix as presented by Lefkovitch (1965) is adopted here. Populations are grouped by stages which can be of unequal duration with no restriction to single year classes. The birth and aging matrix transform for N such stages is given by

$$\begin{bmatrix} P_{i1}^k\ (t+1,3) \\ P_{i2}^k\ (t+1,3) \\ P_{i3}^k\ (t+1,3) \\ \cdot \\ \cdot \\ \cdot \\ P_{iN}^k\ (t+1,3) \end{bmatrix} = \begin{bmatrix} b_{i1} & f_{i2}^k & f_{i3}^k & \cdot & f_{iN}^k \\ a_{i1} & b_{i1} & 0 & \cdot & 0 \\ 0 & a_{i2} & b_{i3} & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot & 1 \end{bmatrix} \begin{bmatrix} P_{i1}^k\ (t+1,2) \\ P_{i2}^k\ (t+1,2) \\ P_{i3}^k\ (t+1,2) \\ \cdot \\ \cdot \\ \cdot \\ P_{iN}^k\ (t+1,2) \end{bmatrix} \qquad (8)$$

where

$P_{ij}^k(t+1,3)$ = density of population i, age class j after accounting for births and aging in compartment k

$P_{ij}^k(t+1,2)$ = density of population i, age class j before accounting for births and aging, but after accounting for spatial redistributions to compartment k

a_{ij} = fraction of population i, age class j advancing to age class $j+1$

b_{ij} = fraction of population i, age class j remaining in age class j

f_{ij}^k = fecundity function for population i, age class j in compartment k.

The coefficients a and b are functions of the size of the time step and the division of ages within the population. Equation (8) also implies a fixed age distribution within an age class, such as a uniform distribution.

The fecundity term, f, is a function of the population age class, as well as being time and space dependent. Explicit population crowding effects are neglected here because they would be comingled with the other density-dependent terms in Equation (4).

Composite Ecosystem Dynamics Equations

The above equations are combined and expressed by the general ecosystem dynamics model given below. The final surviving, redistributed, and aged population vector at the end of the time period has been redefined as $P(t+1) = P(t+1,3)$.

$$P^{k}_{ij}(t+1) = \sum_{n=1}^{N_i} \sum_{m=1}^{M} F^{k}_{ijn}(t)\, g^{mk}_{in}(t)\, S^{m}_{in}(t)\, e^{-\alpha_{in}P^{m}(t)}$$

$$\times\, e^{-\beta_{in}P^{m}(t)} \left[1 - R^{m}_{in}(t)\, e^{-\gamma_{in}P^{m}(t)}\right]$$

$$\times\, P^{m}_{in}(t) \tag{9}$$

where m is summed over all spatial compartments M; n is summed over all population subgroups N_i; and $F^{k}_{ijn}(t)$ is defined by

$$F^{k}_{ijn}(t) = \begin{cases} f^{k}_{in}(t)\,;\; j = 1,\ n \geqq 2 \\ b_{in}(t)\,;\; j \geqq 1,\ n = j \\ a_{in}(t)\,;\; j \geqq 2,\ n = j-1 \\ 0 \qquad ;\ \text{otherwise.} \end{cases} \tag{10}$$

The model parameters in Equations (9) and (10) consist of maximum survival/growth rates (S), starvation mortality rates (R), transport terms (g), fecundity factors (f), age class changes (a and b), and population interaction coefficients (α, β, and γ). Time dependency is indicated for all parameters except the interaction terms. Space dependency is assumed to apply to all but age class changes and interaction terms. If the parameters are described by probabilistic functions, the model becomes a stochastic representation.

The above difference model represents a comprehensive description of coupled fish population dynamics and is proposed for general application. The form of Equation (9) is particularly well suited for computer implementation; it provides an efficient time-step simulation capability without requiring a numerical integration scheme. The model can be conveniently programmed on a mini-computer system and used to simulate complex multispecies population dynamics.

MODEL PARAMETER ESTIMATION IN PRACTICAL APPLICATIONS

The predictive power of the difference model in practical applications is obviously dependent on the knowledge of the ecosystem processes and the ability to estimate the associated parameters used in the modeling. This situation is true for any ecosystem model whether it consists of difference equations, differential equations, or any other formulation. In fact, I (1980) showed that difference equations representing multispecies populations can be used to approximate the complex response modes of differential equations by relating parameters and choosing suitably small differencing time steps. I also showed that the difference model suffers from a similar sensitivity to the parameter estimates; the problem becomes more severe with increasing ecosystem complexity.

Certain parameters in either difference or differential equation models can be roughly estimated from field and/or laboratory studies. Examples include fecundity and growth rates of individual fish which can be observed directly. Population-level parameters, such as interaction and transport terms, are more difficult to estimate given the dynamic, wide-ranging nature of fish behavior. Even with extensive field sampling and the use of multivariate statistical techniques to sort out stochastic environmental features (Reid and Mackay 1968; Mobley 1973; Poole 1976), these parameter estimates will typically have a large degree of uncertainty.

The potential advantage of difference models in dealing with parameter uncertainty is related to their computational efficiency. When parameter uncertainty is represented in a probabilistic framework, Monte Carlo procedures can be applied to statistically describe population response characteristics based on large numbers of simulation runs. Probabilistic descriptions of parameter uncertainty can express both the inherent stochastic nature of the ecosystem and the parameter estimation error. One problem is that the stochastic ecosystem features, which are of primary interest, will typically be masked in the statistics by the large parameter estimation errors if realistic values for the latter are included.

I (1980, in press) used nonlinear programming (NLP) techniques to treat parameter uncertainty in dynamics models for a general class of ecosystem problem. My approach is summarized below; it has been used for resolving parameter estimates in the difference model application discussed in the section that follows.

An NLP problem can be stated in the following general form:

$$\begin{array}{ll} \text{minimize} & f(x) \\ \text{subject to} & g(x) = 0 \\ & x_0 \leqslant x \leqslant x_m \end{array}$$

where x is the variable vector with upper and lower bounds of x_0 and x_m, respectively; $f(x)$ is the so-called objective function; and $g(x)$ is a vector function of implicit constraints.

The problem scenario for my NLP formulation is that of predicting the dynamic response of ecosystem populations to a given perturbation. The response is characterized over some period of interest by the objective function which, depending on the particular problem, can be equated to average population numbers, final population levels, worst-year fishery catch, or some other dynamic feature. The ecological parameters in the dynamics model become the variables with bounds corresponding to the estimated parameter uncertainty range.

Implicit parameter constraints are added to the formulation based on available population history data, ecosystem stability observations, or any known or postulated relationships between parameters. The historical population data are substituted directly into the difference equations, or other assumed dynamics equations. In effect, such constraints force the response modes of the dynamics model to include past population observations, albeit ones that occurred under different (known) conditions than those of interest in the future. Stability observations also infer conditions on the dynamics equations and, hence, model parameters. However, there are practical issues in formulating such conditions. Lyapunov stability analysis techniques (Brogan 1974), while applicable to nonlinear system analysis, are not readily defined for the complex difference equations.

Efficient NLP computational procedures have been applied by me (1980) to solve the special ecosystem formulation described above. A search takes place through bounded parameter space for extreme (minimum and maximum) objective function values while maintaining the equality of the implicit constraints, i.e., the search proceeds on the "constraint surface" in parameter space. The key to an effective problem solution is the computational requirements of the dynamics model which is used in both constraint formulation and for evaluating the objective function at each search step. While the NLP approach does not give definitive estimates of individual model parameters, it strongly delimits their range of values via the interrelationships established by the implicit constraints (Atkinson 1980).

ECOSYSTEM SIMULATIONS USING THE DIFFERENTIAL EQUATION MODEL

The discrete-time multispecies dynamics model given by Equation (9) has been implemented as a FORTRAN computer program and used to perform a variety of simulations of theoretical and applied fisheries scenarios (Atkinson 1980). A case of some practical interest, the collapse of the sardine population within the California Current region, will be described and used to demonstrate the potential model utility.

General Description of the Sardine Population Collapse off California

The waters of the California Current flow southward along the west coast of North America covering the general region are illustrated in Figure 2. While the California Current supports a diverse group of fish, the sardine fishery was by far the most important in the early years of this century until the dramatic collapse of the sardine population in 1930-60. A large increase in fishing effort took place during this time and apparently caused, or at least was associated with the sardine population collapse. The estimated history of the sardine population from 1930 to 1960 as derived by Murphy (1966) is shown in Figure 3.

Two sets of anchovy population estimates for the 1930-60 time frame are also presented in Figure 3. Although these data are confused by significant gaps and strong fluctuations from year to year, there does appear to be a significant population increase from levels in the 1940's and early 1950's to that near the end of the 1950's. Since the anchovy is the chief competitor of the sardine with similar food requirements and overlapping habitat boundaries, the general indication is that the anchovy replaced the sardine within the trophic structure (Murphy 1966; Gulland 1971). Murphy's (1966) 3-yr averaged data provides the clearest evidence of this increasing trend. Smith's (1972) yearly estimates show that the anchovy population actually declined from 1940-41 to 1950 (the next year in which data was available), before a sharp rise occurred. The significant variations evident in both anchovy and sardine data are probably caused by random environmental influences on recruitment success (Lasker 1978; Parrish et al. 1981; Methot 1983).

Soutar and Isaacs (1974) presented some interesting longer term data on the sardine and anchovy (plus other pelagic fish) as derived from sedimentary scale depositions in anaerobic basins off Southern California and Baja California. The deposition rate, which is averaged by 5-yr periods, provides a relative picture of the population variations over the last 150 yr (up to 1970). The data for the 1930-60 time frame indicate similar trends to that above, i.e., decreasing sardine levels and increasing anchovy levels. However, significant sardine and anchovy

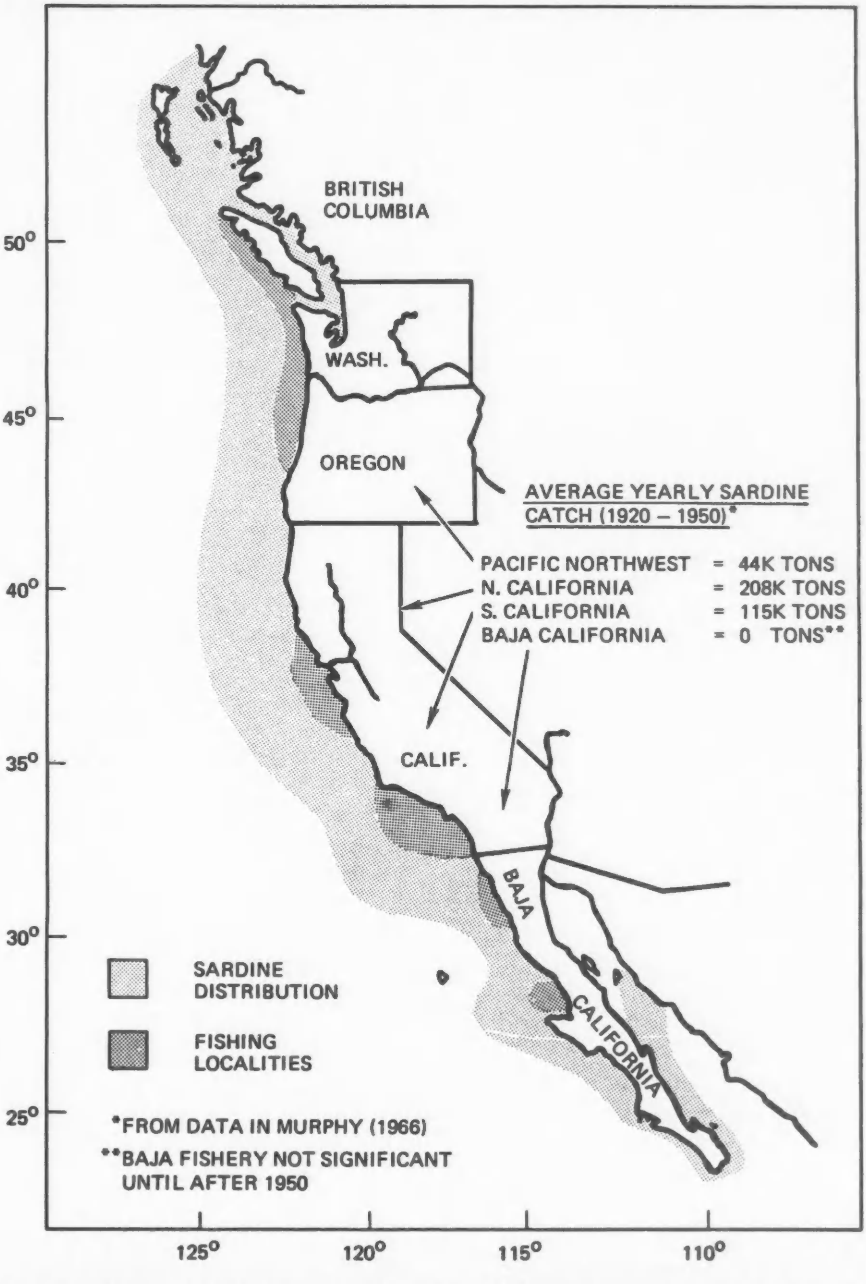

BRITISH COLUMBIA
WASH.
OREGON
CALIF.
BAJA CALIFORNIA
AVERAGE YEARLY SARDINE CATCH (1920 – 1950)*
PACIFIC NORTHWEST = 44K TONS
N. CALIFORNIA = 208K TONS
S. CALIFORNIA = 115K TONS
BAJA CALIFORNIA = 0 TONS**
SARDINE DISTRIBUTION
FISHING LOCALITIES
*FROM DATA IN MURPHY (1966)
**BAJA FISHERY NOT SIGNIFICANT UNTIL AFTER 1950
50°
45°
40°
35°
30°
25°
125°
120°
115°
110°

FIGURE 2.—Map of the California Current region showing sardine distribution and major fishing localities in the period before 1950 (from Murphy 1966).

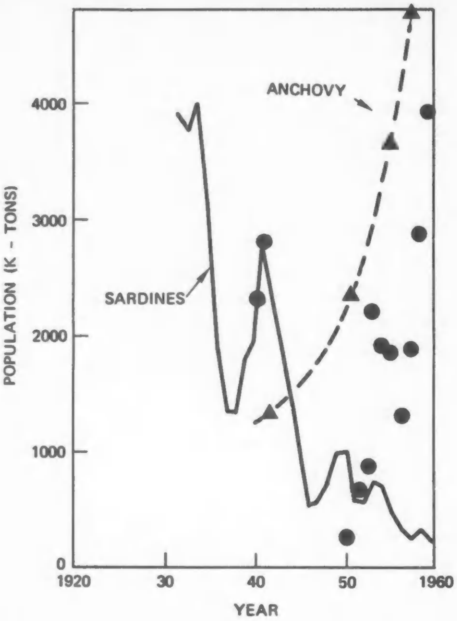


FIGURE 3.—Estimated adult populations of sardine and anchovy during the 1930-60 sardine collapse period. The solid line corresponds to yearly sardine estimates by Murphy (1966). The dashed line with triangles corresponds to 3-yr average anchovy estimates also by Murphy; the initial point is a 2-yr estimate with a data gap until 1951. The circles correspond to yearly anchovy estimates by Smith (1972); a data gap exists between 1941 and 1950.

variations are also evident in earlier times before fishing pressure became a significant factor in the ecosystem. For example, the sardine history showed extremely low levels in 1865-80 comparable to the levels after 1940. The earlier anchovy record, while also having periods of relatively high and low sedimentation rate, appears to have been at consistently higher levels before 1930-60, even higher than the recent increase of the late 1950's. Soutar and Isaacs (1974) stated that relatively unproductive conditions have apparently existed for the past 30 yr or so and have generally affected fish populations of the California Current.

Model Formulation

The waters of the California Current region, with their chemical and biological constituents, can be viewed as an ecological system (Sette 1969). The present model focuses on the sardine and anchovy subsystem defined by Riffenburgh (1969) and shown in Figure 4. While not a comprehensive description of this ecosystem, I use this representation to demonstrate the application of the difference model in a reasonably complex fishery situation. The sardine ecosystem will be simulated during the period from 1932 to 1952 spanning the years of the major sardine collapse.

The sardine population is divided into three age groups: larval-year stages, yearlings, and adults. The larval year is the most vulnerable period of the sardines' development during which it goes through many fundamental changes. The yearlings are the in-between stage to the sexually mature adult members of the population, which are defined to be 2-yr-olds and above. Early stages of the sardine feed on phytoplankton while the adults feed primarily on zooplankton (Huppert et al. 1980). The adults are also predators of their own larval stages and those of the anchovy as indicated in Figure 4.

The anchovy population is divided into two groups, larvae and adult, which have similar intergroup relationships and feeding habits to the corresponding sardine groups. Competitor and predator groups to the sardine and anchovy are defined as lumped assemblages, both encompassing a broad range of diverse fish species; the competitor group also contains many invertebrates. The pelagic fish competitors (e.g., jack mackerel) are assumed to behave similarly to the sardine and anchovy except that some of the larger members feed on the sardine yearling stage (Riffenburgh 1969). The predators (e.g., hake and baracuda) feed on the adults of the sardine-anchovy-competitor trophic level and also have other prey that have been decoupled from the modeled subsystem. Phytoplankton and zooplankton groups are modeled implicitly as carrying capacity terms.

Additional model assumptions are that 1) spatial features are not critical (i.e., one spatial compartment is used), and 2) seasonal effects can be ignored (i.e., a yearly time step is defined). These two assumptions are probably not justifiable in the time period after 1950 or so, because of the shift of dominance from the northern sardine subpopulation to the southern one. Important differences in such factors as natural survival rates, maturation characteristics, and fishing effort exist for these subpopulations (Murphy 1966).

Discrete-Time Difference Equations

The difference model representing the seven interacting populations of the sardine ecosystem is pre-

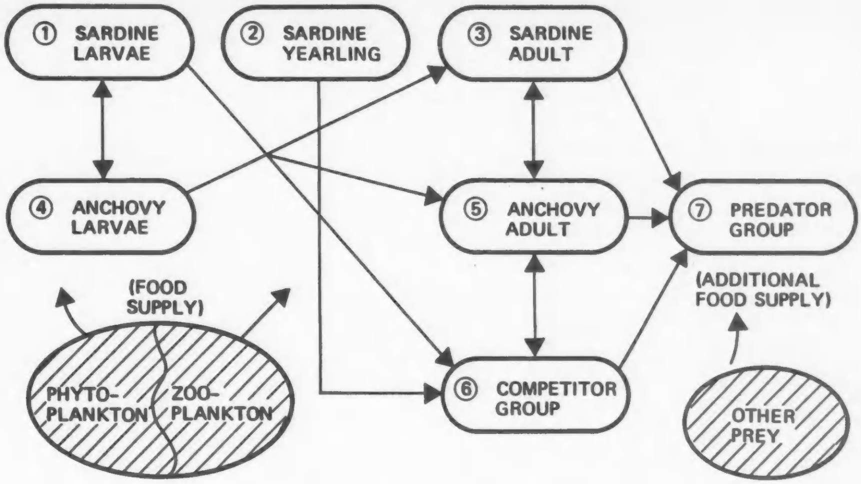


FIGURE 4.—Schematic showing interactions between sardine ecosystem groups as modeled by Riffenburg (1969). Competitive relationships are indicated by the connecting lines with dual arrowheads, while predator-prey relationships are defined by arrows pointing to the predator.

sented in Table 1. These equations reflect the general form of Equation (9) for a single spatial compartment. Parameters are defined for all processes other than transport, including competition, predator-prey, survival/growth, births, and fecundity. These parameters are assumed to be independent of the year during the 1932-52 simulation period, except for 1) the sardine fishing rate, $\delta_3(t)$, and 2) a sardine larvae survival factor, $E_1(t)$. The latter are related to the parameters presented earlier by

$$\delta_3(t) = 1 - S_{f3}(t)$$

$$E_1(t) = S_1(t)/\overline{S}_1$$

where S_{f3} is defined in Equation (5) and $\overline{S}_1$ is the average (reference) sardine larvae survival rate during 1932-52. The time-varying fishing rate and larvae survival factor represent the "drivers" perturbing the ecosystem during the sardine collapse period.

Time-varying representations may also be ap-

TABLE 1—Difference equations describing biomass dynamics of the sardine ecosystem populations. Note that age sub-groups are indexed as separate populations to simplify the nomenclature. Also, all populations in exponentials are assumed to be at time *t*.

Population 1 - sardine larvae

$$P_1(t+1) = f_3 S_{3,0}\,[1 - \delta_3(t)]\,\exp(-\alpha_{33}P_3 - \alpha_{35}P_5 - \alpha_{36}P_6)\,\exp(-\beta_{37}P_7)P_3(t)$$

Population 2 - sardine yearling

$$P_2(t+1) = E_1(t)S_1\,\exp(-\alpha_{11}P_1 - \alpha_{14}P_4)\,\exp(-\beta_{13}P_3 - \beta_{15}P_5 - \beta_{16}P_6)P_1(t)$$

Population 3 - sardine adult

$$\begin{aligned} P_3(t+1) = {} & S_2\,\exp(-\alpha_{22}P_2 - \alpha_{25}P_5)\,\exp(-\beta_{26}P_6)P_2(t) \\ & + S_{3,0}[1 - \delta_3(t)]\,\exp(-\alpha_{33}P_3 - \alpha_{35}P_5 - \alpha_{36}P_6)\,\exp(-\beta_{37}P_7)P_3(t) \end{aligned}$$

Population 4 - anchovy larvae

$$P_4(t+1) = f_5 S_5\,\exp(-\alpha_{53}P_3 - \alpha_{55}P_5 - \alpha_{56}P_6)\,\exp(-\beta_{57}P_7)P_5(t)$$

Population 5 - anchovy adult

$$\begin{aligned} P_5(t+1) = {} & S_4\,\exp(-\alpha_{41}P_1 - \alpha_{44}P_4)\,\exp(-\beta_{43}P_3 - \beta_{45}P_5 - \beta_{46}P_6)P_4(t) \\ & + S_5\,\exp(-\alpha_{53}P_3 - \alpha_{55}P_5 - \alpha_{56}P_6)\,\exp(-\beta_{57}P_7)P_5(t) \end{aligned}$$

Population 6 - competitor group

$$P_6(t+1) = S_6\,\exp(-\alpha_{63}P_3 - \alpha_{65}P_5 - \alpha_{66}P_6)\,\exp(-\beta_{67}P_7)P_6(t)$$

Population 7 - predator group

$$P_7(t+1) = S_7\,\exp(-\alpha_{77}P_7)\,[1 - R_7\,\exp(-\gamma_{73}P_3 - \gamma_{75}P_5 - \gamma_{76}P_6)]\,P_7(t)$$

propriate for other population parameters such as anchovy larvae survival but are ignored here. The modeling emphasizes those features directly impacting the adult sardine population because it is the only population for which detailed data are available for making comparisons.

Initial Conditions: State of the Ecosystem

The sardine ecosystem will assumed to be in an approximate equilibrium state prior to 1932, ignoring random population fluctuations. The sardine population appears to be consistently near virgin levels for the few years that data are available before 1932 (Fig. 3), and I speculate that the other populations are at reasonably consistent levels as well. There is some justification for overall stability at the sardine-anchovy-competitor trophic level and the predator trophic level, if not for individual fish species or population groups (Sette 1969; Steele 1979).

Estimates of population biomasses prior to the 1932-52 collapse period were summarized by Atkinson (1980) from data given by Murphy (1966) and Riffenburgh (1969). The biomasses presented below correspond to the assumed equilibrium state at the start of a fishing year. A fishing year is defined to begin in the summer after the main spring spawning season of the sardine and anchovy.

- sardine larvae $\bar{P}_1$ = 1,600 kilotons
- sardine yearling $\bar{P}_2$ = 300 kilotons
- sardine adult $\bar{P}_3$ = 4,000 kilotons
- anchovy larvae $\bar{P}_4$ = 400 kilotons
- anchovy adult $\bar{P}_5$ = 1,000 kilotons
- competitors $\bar{P}_6$ = 3,000 kilotons
- predators $\bar{P}_7$ = 2,000 kilotons

The initial state in 1932 is also defined by this biomass vector, $\bar{P}$.

Parameter Estimation for the Sardine Ecosystem Model

First, I point out that the above model representation is not intended to be a comprehensive description of the sardine ecosystem or to have general application for predicting future population dynamics, at least not as developed here. However, it is proposed as a reasonable representation to demonstrate the similarity between simulated results and observed system dynamics during the 1932-52 time frame provided appropriate parameter estimates can be determined. The value of the difference formation in dealing with the parameter uncertainty issue will be illustrated in the discussion below of parameter estimation procedures.

Two model parameters in the equations of Table 1 were estimated directly from available data in the literature (Murphy 1967; MacCall 1979; Clark and Phillips 1932; Huppert et al. 1980): adult sardine survival, $S_{3,0}$ = 1.40 (excludes fishing mortality effects), and adult anchovy survival, S_5 = 1.20. The driver terms in the model, $\delta_3(t)$ and $E_1(t)$, were also estimated from available data during the simulation period. These terms could not, of course, be definitized without the benefit of present hindsight. In a predictive situation, such terms would generally have a large degree of uncertainty, because projected fishing pressure is highly speculative while larvae survival has a strong stochastic component. Here, however, the available data will be used to the extent possible to resolve model terms.

Estimates of sardine fishing parameter, $\delta_3(t)$, were derived from Murphy's (1966) data and are shown plotted in Figure 5. The simplified model used in the simulations ignores detailed yearly variations and focuses on the major trends. A linear increase is assumed during the period from a rate of about 0.1 in 1932 to a rate >0.4 in 1936. The fishing rate is assumed to remain constant for the remainder of the simulation period.

The assumed model for the sardine larvae survival term, $E_1(t)$, is presented in Figure 6 along with Sette's (1969) data from which it was derived. These data represent numbers of fish at age class two versus the year spawned. The survival rate model assumes that these observed fluctuations in the data primarily reflect random survival effects during the first year of life. $E_1(t)$ was obtained by normalizing Sette's data with respect to the spawning population biomass and defining a relative scale such that the integrated value over the 20-yr period from 1932 to 1952 was equal to one.

The remaining model parameters, which represent the great majority of those in the equations of Table 1, could not be directly estimated to any degree of accuracy from available literature data. Instead, these estimates were derived from the special nonlinear programming analysis of mine (1980, in press) mentioned previously. I treated these ecosystem model parameters as variables with upper and lower bounds reflecting their uncertainty ranges. The bounds established by me for the sardine ecosystem parameters were typically an order of magnitude. Implicit parameter constraints were

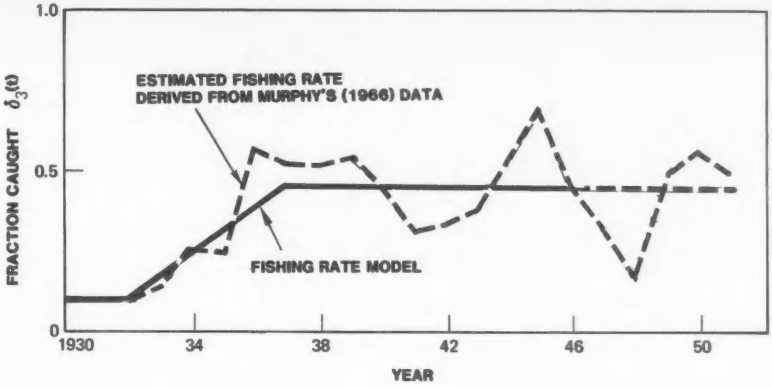


FIGURE 5.—Model of sardine fishing rate, $\delta_3(t)$, used in the sardine ecosystem simulations.

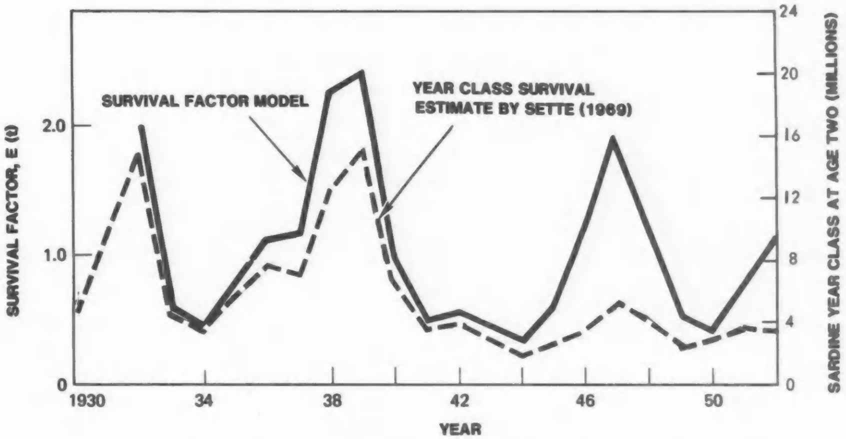


FIGURE 6.—Model of sardine larvae survival, $E_1(t)$, used in the sardine ecosystem simulations.

defined by the assumed equilibrium condition prior to 1932-52. Setting the time-varying fishing rate at its pre-1932 value ($\delta_3 = 0.10$) and fixing the time-varying larval survival factor at its reference value ($E_1 = 1.0$), a set of seven equality constraints were specified corresponding to the seven population equations in Table 1 with $P(t + 1) = P(t) = \bar{P}$. While there is still significant degrees-of-freedom in the model (i.e., more parameters than equality constraints), I was able to greatly resolve their values based on my nonlinear programming procedures.

The parameters in Table 2 represent the "nominal" estimates presented by me (1980) based on my NLP analyses. In searching for minimum and maximum population response levels throughout bounded parameter space, a series of intermediate search steps were taken that produced suites of interdependent parameter values satisfying the pre-1932 equilibrium condition. Population response levels were equated to the average sardine population during the 1932-52 simulation period in this analysis. The selected nominal parameter suite in Table 2 gives response levels approximately midway between the determination of minimum and maximum levels.

Note that the parameter values in Table 2 were not derived from statistical procedures using the

TABLE 2.—Estimated values of the sardine ecosystem model parameters (from Atkinson 1980).

Population	Parameter type	Symbol	Nominal value
1 Sardine larvae	Survival/growth	S_1	7.26
	Competition	α_{11}	5×10^{-6}
	Competition	α_{14}	2.5×10^{-6}
	Predation	β_{13}	7.6×10^{-4}
	Predation	β_{15}	3.8×10^{-4}
	Predation	β_{16}	7.6×10^{-5}
2 Sardine yearling	Survival/growth	S_2	2.10
	Competition	α_{22}	3.7×10^{-5}
	Competition	α_{25}	1.8×10^{-5}
	Predation	β_{26}	1.8×10^{-5}
3 Sardine adult	Survival/growth	$S_{3,0}$	1.40
	Competition	α_{33}	1.5×10^{-5}
	Competition	α_{35}	1.0×10^{-5}
	Competition	α_{36}	5.0×10^{-6}
	Predation	β_{37}	1.0×10^{-4}
	Fecundity	f_3	0.468
4 Anchovy larvae	Survival/growth	S_4	0.50
	Competition	α_{41}	2.5×10^{-6}
	Competition	α_{44}	5.0×10^{-6}
	Predation	β_{43}	1.5×10^{-4}
	Predation	β_{45}	3.0×10^{-4}
	Predation	β_{46}	3.0×10^{-5}
5 Anchovy adult	Survival/growth	S_5	1.30
	Competition	α_{53}	2.0×10^{-5}
	Competition	α_{55}	3.0×10^{-5}
	Competition	α_{56}	1.0×10^{-5}
	Predation	β_{57}	1.0×10^{-4}
	Fecundity	f_5	0.432
6 Competitor group	Survival/growth	S_6	1.65
	Competition	α_{63}	5.0×10^{-5}
	Competition	α_{65}	5.0×10^{-5}
	Competition	α_{66}	5.0×10^{-5}
	Predation	β_{67}	5.0×10^{-5}
7 Predator group	Survival/growth	S_7	1.23
	Mortality	R_7	0.5
	Competition	α_{77}	5.2×10^{-5}
	Prey	γ_{73}	2.5×10^{-4}
	Prey	γ_{75}	2.5×10^{-4}
	Prey	γ_{76}	1.25×10^{-4}

population data during the simulation period (Fig. 3). The estimates are uncoupled from these data and, hence, reflect strictly a priori knowledge as would exist in applications where predictions are required. Furthermore, the parameter values are not proposed as best estimates of these parameters, but simply provide a consistent set of values for use in the simulation demonstration. The nonlinear programming approach of mine is structured in general to bound future ecosystem response characteristics given only a priori population data.

Ecosystem Simulations

The simulated sardine ecosystem histories are presented and compared with estimated sardine and anchovy population data in Figure 7. The adult sardine population simulation is in reasonably good agreement with the data of Murphy (1966) giving the many approximations and simplifying assumptions used in the modeling. The major dynamic features of the adult sardines decline are consistent, including the sharp rebounds associated with the favorable conditions for sardine larvae survival in 1938 and 1939 and again in 1947 (Fig. 6).

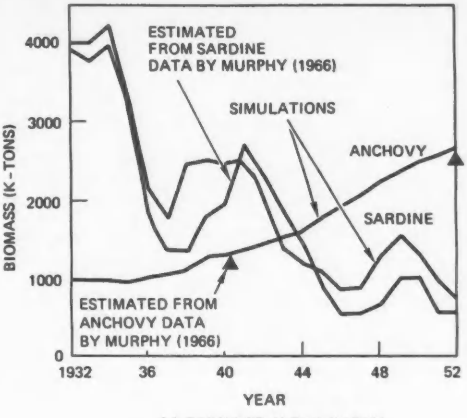
The simulated anchovy response in Figure 7, which ignores any fluctuating larvae survival component, appears to track the 3-yr averaged estimates of Murphy (1966). The anchovy population increases along with the competitor group to fill the ecological void in this trophic level. The predator biomass decreased slightly because the decline of the sardine results in a less desirable food supply, at least according to estimated input parameters. Unfortunately, there are no available data for comparing with the predicted competitor and predator group responses.

Another simulation run was made to investigate the speculation that fluctuating larval survival rates, by themselves, might have caused the sardine collapse. The sardine fishing rate was held at the relatively low levels that existed before 1932 (δ_3 = 0.10), and the fluctuating larvae survival model in Figure 6 was applied. The resulting simulation run is presented in Figure 8 and shows the predicted history of the adult sardine population, along with that of the anchovy, competitor, and predator groups. The adult sardine population again fluctuates markedly but now remains at relatively high levels, in no apparent danger of collapsing. It would appear from these runs that the added fishing pressure is necessary to explain the actual event during this period.

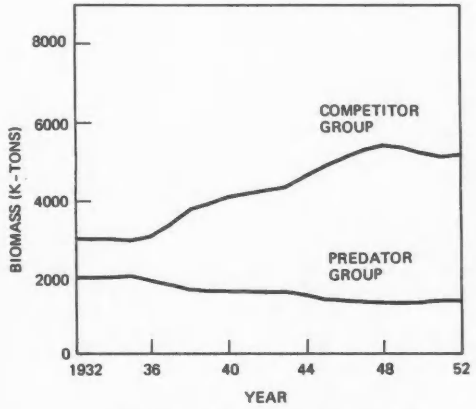
CONCLUSIONS

A general set of discrete-time difference equations have been developed for use in simulating the important dynamic processes effecting fish populations, including

- interactions between competors, predators, and prey
- birth, growth, and aging processes within a



(a) SARDINES AND ANCHOVY



(b) COMPETITOR AND PREDATOR GROUPS

FIGURE 7.—Simulation run for assumed models of increased sardine fishing rate and fluctuating sardine larvae survival rate.

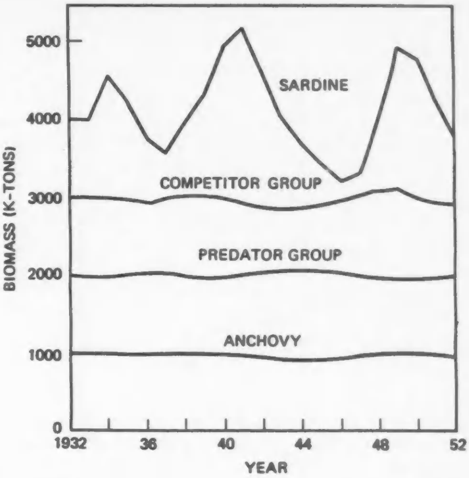


FIGURE 8.—Simulation run for assumed constant pre-1932 fishing rate but with fluctuating sardine larvae survival rate.

single population group
- spatial and temporal variations.

The sardine subsystem within the California Current region was modeled using the multispecies difference model and simulations computed for the sardine's collapse period of 1932-52. Input drivers perturbing the system included representations of the increased sardine fishing pressure and the fluctuating sardine larvae survival rates during this period. Simulation results were shown to compare favorably with the available population history data. The increased fishing pressure was indicated to be the fundamental cause for the sardine collapse; the estimated yearly fluctuations in sardine larvae survival could not by themselves have caused this sudden event.

These simulation results demonstrate the use of the discrete-time difference model as an efficient simulation tool. There appear to be many applications for the model in theoretical and applied multispecies fisheries studies.

ACKNOWLEDGMENTS

This work was based on a part of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree at the University of California, Los Angeles. S. E. Jacobsen, chairman of the dissertation committee, provided guidance and encouragement throughout these studies. D. A. Kiefer of the Department of Biological Sciences, University of Southern California, reviewed early versions of this paper and made helpful comments.

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FECUNDITY OF NORTHERN SHRIMP, *PANDALUS BOREALIS*, (CRUSTACEA, DECAPODA) IN AREAS OF THE NORTHWEST ATLANTIC

D. G. PARSONS AND G. E. TUCKER[1]

ABSTRACT

Fecundity of the northern shrimp, *Pandalus borealis*, and relationships between number of eggs and carapace length were determined from 15 samples taken in 9 areas of the Northwest Atlantic. The sampling area extended from Davis Strait to the south coast of Newfoundland. Comparisons of samples suggested that fecundity levels can vary between seasons, years, and areas. A relationship between egg production and environmental temperature was not evident from available samples.

The northern or pink shrimp, *Pandalus borealis*, is a protandric hermaphrodite with a circumboreal distribution. In the Northwest Atlantic, it occurs from about lat. 75°N at West Greenland to about lat. 42°N at Georges Bank (Squires 1970). Fecundity of this species in the North Atlantic has been studied in southern Norway (Rasmussen 1953), northern Norway (Thomassen 1977), the North Sea (Allen 1959), Iceland (Skúladóttir et al. 1978), West Greenland (Horsted and Smidt 1956), Barents Sea (Teigsmark 1983), and Gulf of Maine (Haynes and Wigley 1969). Bottom water temperatures recorded at depths where shrimp samples were collected during these studies varied considerably between areas but were within the range of tolerance for survival of adults as reported by Allen in 1959 (−1.68° to 11.13°C).

This paper provides information on the fecundity of *P. borealis* in the Northwest Atlantic. Samples were collected in areas of known shrimp concentration off Baffin Island, in the eastern Hudson Strait and Labrador Sea, and off the south coast of Newfoundland. Bottom temperatures at sampling sites also varied between these areas but were confined to the lower half of the tolerance range (<7°C). Comparisons are made between selected combinations of the data sets presented. The possible effects of ambient temperature on fecundity levels also are considered.

MATERIALS AND METHODS

Samples of ovigerous female shrimp were collected opportunistically during various research cruises conducted by or for the Department of Fisheries and Oceans, St. John's, Newfoundland, Canada, between 1971 and 1982. A total of 15 samples was selected for analysis. These were taken from the Baffin Island area (east of Cumberland Sound); Hudson Strait; North Labrador Sea; Hopedale, Cartwright, and Hawke Channels (on the Labrador Shelf); St. Mary's Bay; Fortune Bay; and the Southwest Newfoundland coast (Fig. 1). For some areas, only one sample was available while for others, samples were obtained in different months and/or different years (Table 1).

Only animals in good condition were selected from the trawl catches for the study (i.e., no noticeable damage and egg mass undisturbed). Individuals were selected over the complete size range of females, preserved in 10% Formalin[2] and returned to the laboratory. It was assumed that within any length group the selection (in terms of number of eggs) was random.

Oblique carapace lengths were measured to the nearest 0.1 mm using Vernier calipers. This measurement is the distance between the posterior margin of the orbit of the eye and the posterodorsal margin of the carapace (Rasmussen 1953).

All eggs were removed from the pleopods, spread in a Petrie dish, and oven dried overnight at 60°C. After drying, eggs were further separated and counted.

Accuracy of the counts was determined by recounting the eggs from 49 animals. Differences from the initial counts in 48 cases varied between −5.75%

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[1] Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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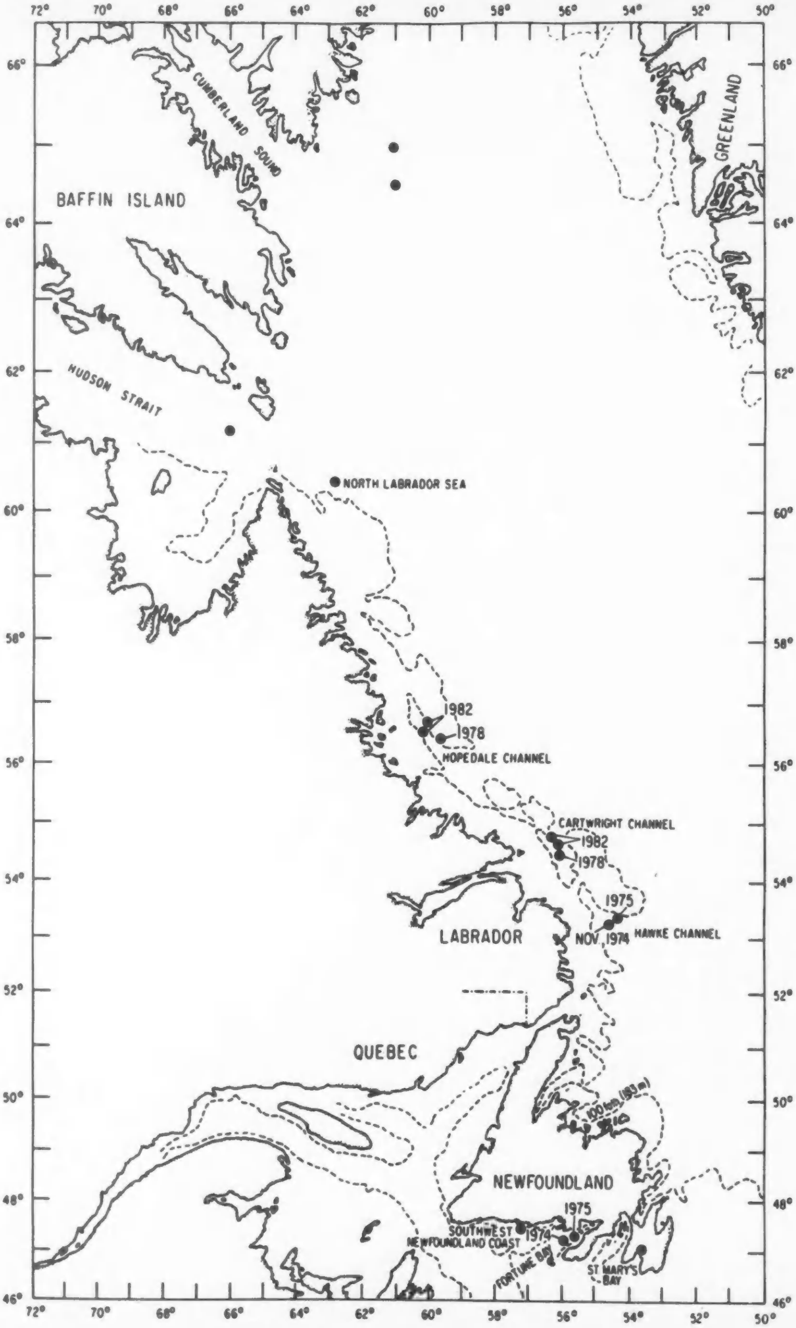

72°
70°
68°
66°
64°
62°
60°
58°
56°
54°
52°
50°
66°
64°
62°
60°
58°
56°
54°
52°
50°
48°
46°
CUMBERLAND SOUND
GREENLAND
BAFFIN ISLAND
HUDSON STRAIT
NORTH LABRADOR SEA
1982
1978
HOPEDALE CHANNEL
CARTWRIGHT CHANNEL
1982
1978
1975
NOV. 1974
HAWKE CHANNEL
LABRADOR
QUEBEC
100 fm (183 m)
NEWFOUNDLAND
1975
SOUTHWEST
NEWFOUNDLAND COAST
1974
FORTUNE BAY
ST. MARY'S BAY

TABLE 1.—Regression equations for fecundity (F) vs. length (L) for *Pandalus borealis* in the Northwest Atlantic.

Sample	Date	*N*	Regression equation	r^2	Temp. °C
Baffin Island	14 Aug. 1978	48	$\log_{10} F = 3.0955 \log_{10} L - 1.1417$	0.75	0.7-1.8
Hudson Strait	13 Sept. 1982	24	$\log_{10} F = 3.8880 \log_{10} L - 2.3967$	0.33	0.6
North Labrador Sea	22 Sept. 1982	43	$\log_{10} F = 3.2715 \log_{10} L - 1.4550$	0.45	0.5
Hopedale Channel	28 Sept. 1978	46	$\log_{10} F = 2.8045 \log_{10} L - 0.7202$	0.70	3.0
Hopedale Channel	11, 25 Sept. 1982	96	$\log_{10} F = 2.8884 \log_{10} L - 0.8893$	0.74	3.2
Cartwright Channel	20 Sept. 1978	45	$\log_{10} F = 3.1824 \log_{10} L - 1.3059$	0.74	3.0
Cartwright Channel	11, 26 Sept. 1982	87	$\log_{10} F = 2.5240 \log_{10} L - 0.3750$	0.68	2.0-2.4
Hawke Channel	24 Aug. 1974	20	$\log_{10} F = 3.4614 \log_{10} L - 1.6670$	0.70	—
Hawke Channel	30 Nov. 1974	24	$\log_{10} F = 1.4613 \log_{10} L + 1.1015$	0.31	2.9
Hawke Channel	23 Sept. 1975	27	$\log_{10} F = 3.0106 \log_{10} L - 1.0147$	0.68	2.7
St. Mary's Bay	18 Mar. 1971	48	$\log_{10} F = 2.3954 \log_{10} L - 0.3691$	0.53	—
St. Mary's Bay	28 Feb. 1974	44	$\log_{10} F = 2.5290 \log_{10} L - 0.5476$	0.47	—
Fortune Bay	17 Mar. 1978	48	$\log_{10} F = 3.0413 \log_{10} L - 1.1187$	0.57	1.0
Fortune Bay	30 Mar. 1979	47	$\log_{10} F = 2.6870 \log_{10} L - 0.6428$	0.70	—
SW Newfoundland Coast	27 Feb. 1978	48	$\log_{10} F = 2.8557 \log_{10} L - 0.7396$	0.78	6.2

and +5.65%. The difference between the total number of eggs counted and recounted was only −0.22% of the initial count. A recount of eggs from one female indicated a difference of −9.38%. It is possible that, in this case, some of the eggs were inadvertently lost between counts.

Parameters for the relationship between number of eggs and carapace length for each sample were determined by linear regression using log-log (base 10) transformation. Some data sets were compared by analysis of covariance, assuming homoscedasticity. All statistical analyses were performed using the REG (regression) and GLM (general linear models) procedures of SAS (Statistical Analysis System).

It must be stressed that samples were obtained opportunistically and not according to a predetermined sampling design. Consequently, the statistical analyses were performed based on a practical approach rather than attempting methods for which strict sampling procedures are required. It was anticipated that differences in fecundity-length relationships could be due to seasonal, annual, and areal effects. Our data only permitted simple comparisons, investigating each factor separately.

Bottom temperatures at most sample locations were recorded to the nearest 0.1°C using either manual or expendable bathythermographs.

RESULTS

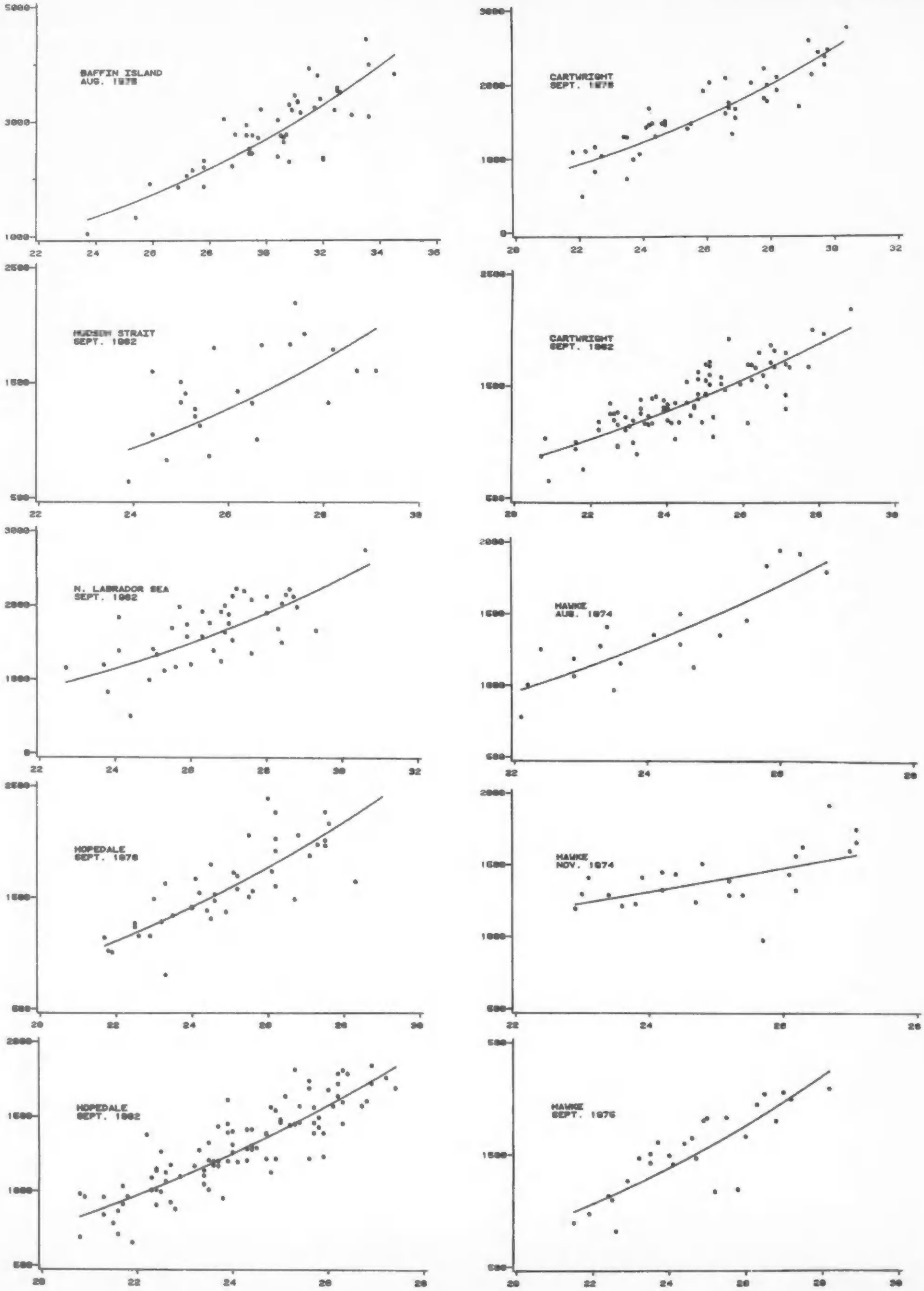
The parameters of the fecundity-carapace length relationships for all 15 samples are given in Table 1. Data and the fitted line for each sample are displayed in Figure 2. Coefficients of determination ranged from 0.31 to 0.78 and all relationships were significant (differences from zero slope were highly significant). Intercepts for the log transformed data were less than zero in all but one case. Slopes ranged from 2.4 to 3.9 except for the sample with positive intercept (1.5).

Only two samples were available (Hawke Channel, August and November 1974) for comparison of fecundity between seasons. Analysis of covariance on the log of both variables indicated a highly significant difference in slopes (Table 2). The data showed that larger females (>24 mm), on average, carried more eggs in August whereas smaller females showed higher fecundity in November (Fig. 3).

Samples from specific areas and seasons were compared to determine similarities or differences between years. Five simple comparisons were possible: St. Mary's Bay - March 1971 vs. February 1974, Hawke Channel - August 1974 vs. September 1975, Fortune Bay - March 1978 vs. March 1979, Cartwright Channel - September 1978 vs. September 1982, and Hopedale Channel - September 1978 vs. September 1982.

No significant differences in either the rate of increase in fecundity with increasing size (slope) or mean number of eggs produced (intercept) were detected between years in three of the five areas compared (Table 2). These were St. Mary's Bay, 1971 and 1974; Hawke Channel, 1974 and 1975; and Fortune Bay, 1978 and 1979 (Fig. 4a, b, and c, respectively). Samples from Cartwright Channel from September 1978 and 1982 showed a significant difference in slopes at $\alpha = 0.05$ (Fig. 4d) whereas samples from the Hopedale Channel for the same

FIGURE 1.—Positions of stations in the northwest Atlantic where northern shrimp fecundity samples were collected.


BAFFIN ISLAND
AUG. 1978
5000
3000
1000
22
24
26
28
30
32
34
36
CARTWRIGHT
SEPT. 1978
3000
2000
1000
0
20
22
24
26
28
30
32
HUDSON STRAIT
SEPT. 1982
2500
1500
500
22
24
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CARTWRIGHT
SEPT. 1982
2500
1500
500
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22
24
26
28
30
N. LABRADOR SEA
SEPT. 1982
3000
2000
1000
0
22
24
26
28
30
32
HAWKE
AUG. 1974
2000
1500
1000
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22
24
26
28
HOPEDALE
SEPT. 1976
2500
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HAWKE
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HAWKE
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30

years were similar in slope but different in elevation (Fig. 4e). Average fecundity at length was higher in 1978 than in 1982 in the latter area.

Three comparisons were possible to detect differences between areas. In 1982, four areas were sampled during September: Hudson Strait, North Labrador Sea, Hopedale Channel, and Cartwright Channel. Analysis of the data indicated no difference in the rate of increase in fecundity with increasing size but a highly significant difference in the mean number of eggs produced (Table 2, Fig. 5a). *T*-Tests for sample means showed that the sample from Hudson Strait was different from those taken off the Labrador coast (Table 3). Fecundity in the former was less at comparable sizes.

Three areas were sampled in August and September 1978: east of Baffin Island (August), Hopedale and Cartwright Channels (September). The data from these samples also were similar in slope but different in elevations (Table 2, Fig. 5b). *T*-tests showed that the lower fecundity observed in the Cartwright Channel was significantly different ($\alpha = 0.05$) from that observed in the other two areas (Table 3).

Two samples were taken off the south coast of Newfoundland early in 1978: one from the southwest coast in February and the other from Fortune Bay in March. Eggs in both samples were "eyed", indicating late stage development. The data showed that average egg production was higher off the southwest coast over the range of sizes compared (Fig. 5c). The statistical analysis indicated similarity in slopes but a highly significant difference in elevations (Table 2).

DISCUSSION

Loss of eggs over the ovigerous period has been reported in previous studies on fecundity of *P. borealis* (Elliot 1970[3]; Ito 1976; Skúladóttir et al. 1978; Stickney and Perkins 1979; Stickney 1981). This loss could be incidental or due to incomplete fertilization and/or disease. Egg diameter also increases between spawning and hatching (Haynes and Wigley 1969; Ito 1976), and some eggs that are

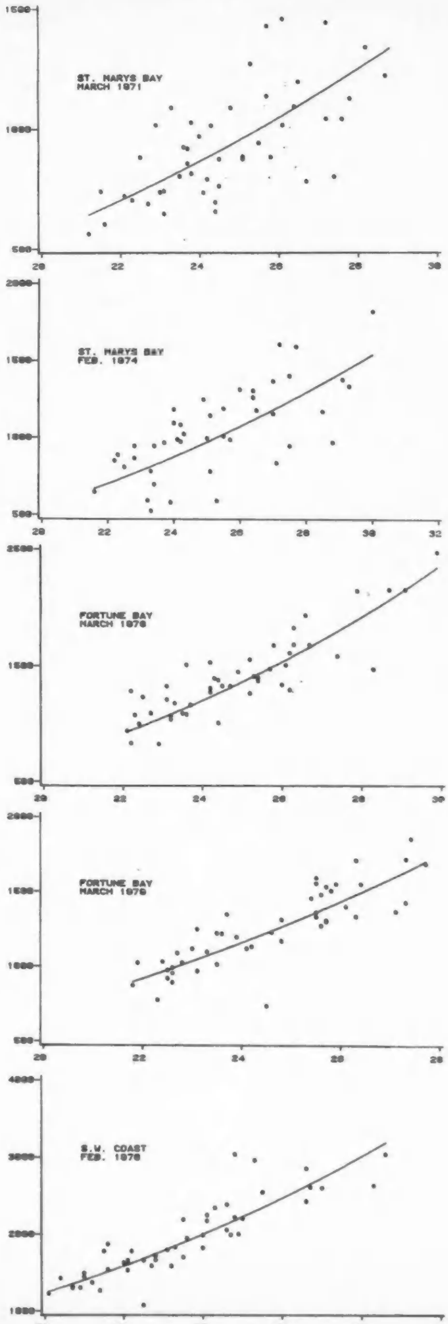

FIGURE 2.—Number of eggs (vertical axis) vs. carapace length in mm (horizontal axis) for 15 samples of female northern shrimp taken from areas of the northwest Atlantic.

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[3] Elliot, D. L. 1970. Fecundity of the northern shrimp, *Pandalus borealis*. Unpubl. manuscr., 32 p. Bowdoin University, Brunswick, ME 04011.

TABLE 2.—Analyses of covariance for fecundity-length relationships.

Effect	Comparison		Slopes F-value	Slopes Prob.	Intercepts F-value	Intercepts Prob.
Season	Hawke Channel	08/74 vs.				
	Hawke Channel	11/74	8.19	0.0067		
Year	St. Mary's Bay	03/71 vs.				
	St. Mary's Bay	02/74	0.06	0.8024	0.18	0.6748
	Hawke Channel	08/74 vs.				
	Hawke Channel	09/75	0.42	0.5215	2.30	0.1367
	Fortune Bay	03/78 vs.				
	Fortune Bay	03/79	0.52	0.4707	1.23	0.2709
	Cartwright Channel	09/78 vs.				
	Cartwright Channel	09/82	4.27	0.0408	0.43	0.5141
	Hopedale Channel	09/78 vs.				
	Hopedale Channel	09/82	0.07	0.7861	26.31	0.0001
Area	Hudson Strait	09/82 vs.				
	North Labrador Sea	09/82 vs.				
	Hopedale Channel	09/82 vs.				
	Cartwright Channel	09/82	1.78	0.1490	10.69	0.0001
	Baffin Island	08/78 vs.				
	Hopedale Channel	09/78 vs.				
	Cartwright Channel	09/78	0.49	0.6140	8.51	0.0003
	SW Newfoundland Coast	02/78 vs.				
	Fortune Bay	03/78	0.17	0.6792	61.32	0.0001

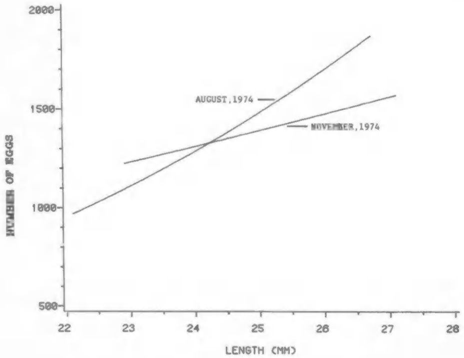

FIGURE 3.—Comparisons of northern shrimp fecundity between seasons for the Hawke Channel, based on predicted values from equations in Table 1.

TABLE 3.—Paired comparisons for area differences when *k* (no. of samples) >2.

		P values for H_0: $\text{Mean}_i = \text{mean}_j$			
Date/sample	No.	1	2	3	4
September 1982					
Hudson Strait	1	·			
North Labrador Sea	2	0.0002	·		
Hopedale Channel	3	0.0001	0.2141	·	
Cartwright Channel	4	0.0001	0.0695	0.4525	·
August 1978					
Baffin Island	1	·			
Hopedale Channel	2	0.5709	·		
Cartwright Channel	3	0.0121	0.0002	·	

close to the periphery and loosely attached may be simply "crowded out".

The evidence of egg loss described in previous studies is sufficient to suggest that combining data from different times of year is not appropriate. The two samples compared in this study produced inconclusive results in that average fecunity was not consistently lower over the complete size range in November compared with the August sample.

Annual variation in fecundity-length relationships occurred in two of five areas sampled in different years. The rate of increase in number of eggs with increasing size only differed significantly in one case, however. The reasons why fecundity differs between years are not known but could be related to changes in environmental conditions and/or egg disease (Stickney 1981). In support of the latter, it is noted that the proportion of nonviable eggs in the 1982 Hopedale Channel sample was higher than in the 1978 sample by an order of magnitude (D. G. Parsons unpubl. data). Fecundity was significantly higher in the 1978 data.

Teigsmark (1983) found that variation within a population during successive years is as great as the variation between populations in a single year and was unable to make a conclusive statement about fecundity of different populations of *P. borealis* in the Barents Sea. He speculated that such differences could be related to availability of food and population density.

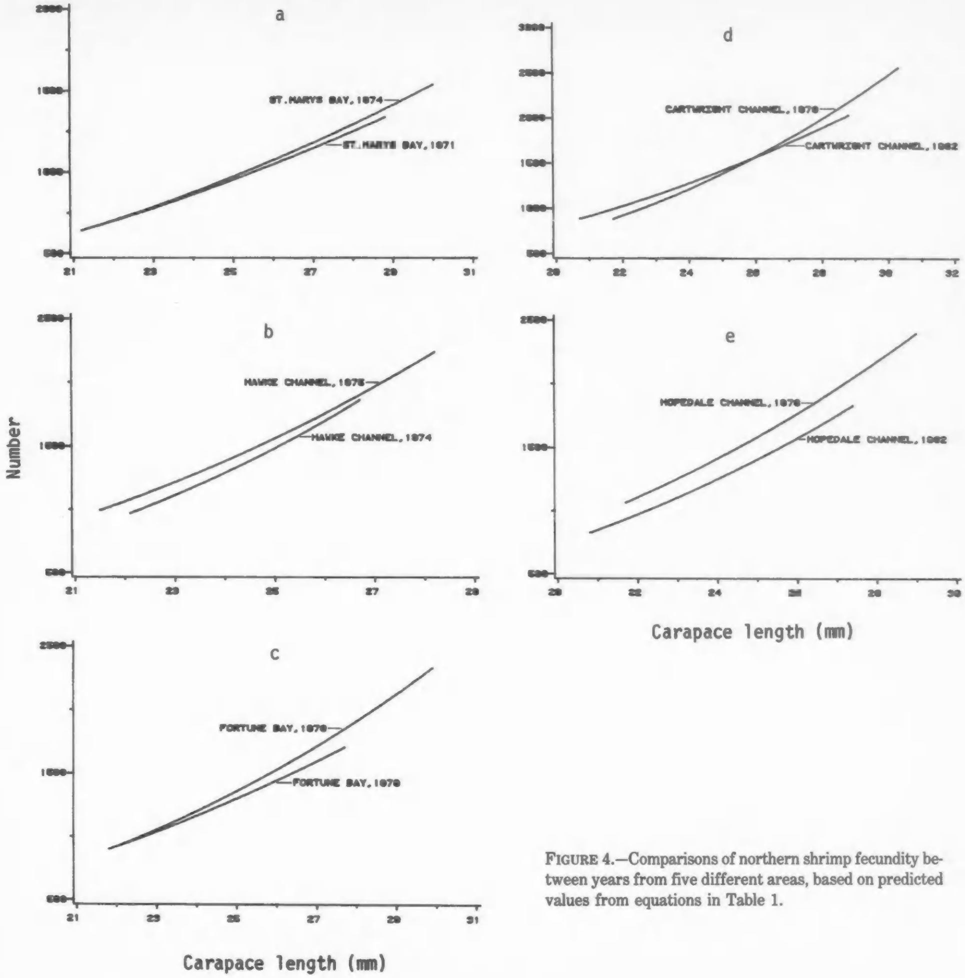

FIGURE 4.—Comparisons of northern shrimp fecundity between years from five different areas, based on predicted values from equations in Table 1.

Based on the comparison of samples taken in 1982, it was shown that the fecunity-length relationships in three areas off Labrador were similar. Similarity was not apparent in 1978 samples which showed that fecundity in the Cartwright Channel was lower than in the Hopedale Channel. This discrepancy in results from Labrador is due to annual differences demonstrated for both channels in 1978 and 1982 samples.

The comparison by area for the 1978 data also implied similarity between the Baffin Island and Hopedale Channel samples. However, the size ranges compared were not the same. Female shrimp ranged in size from 23.7 to 34.5 for the Baffin Island sample in contrast to 21.7 to 29.0 for the Hopedale Channel sample. These differences in size likely reflect separate rates of growth and maturity in the two areas. Therefore, from a biological viewpoint, all three areas sampled in 1978 exhibited different fecundity-length relationships.

The differences between areas, described above, can be considered in relation to the temperatures present in these areas. The bottom temperature at the sampling station off the southwest coast of Newfoundland was 6.2°C, the warmest of all areas sampled (Table 1). The temperature recorded in

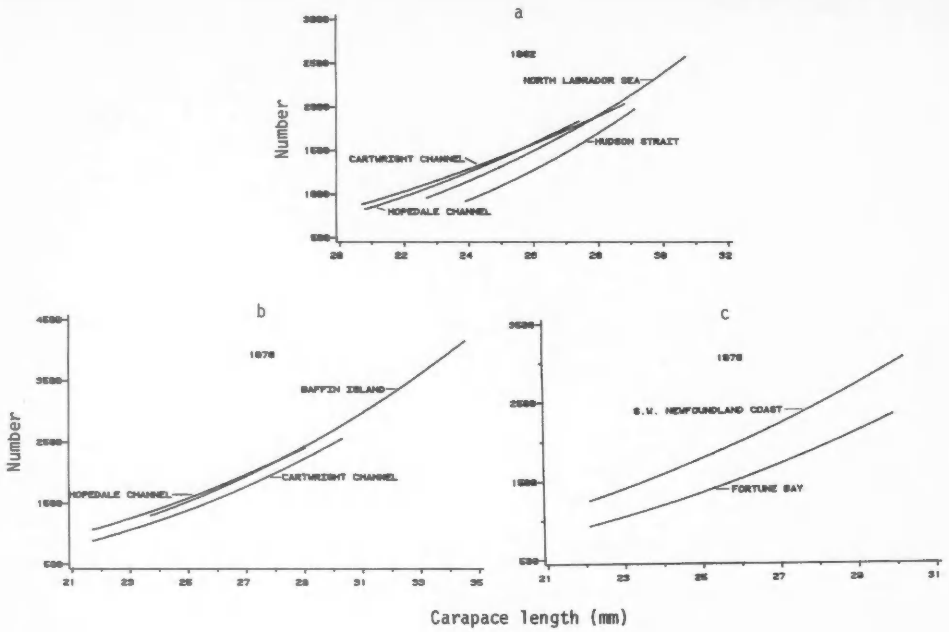

FIGURE 5.—Comparisons of northern shrimp fecundity between areas in 1982 and 1978, based on predicted values from equations in Table 1.

March 1978 in Fortune Bay was 1.0°C, one of the coldest areas. According to Squires (1968), the penetration of Atlantic water into the former area accounts for these warmer temperatures which persist throughout the year. In Fortune Bay, however, the deep bottom water is of mixed Atlantic and Arctic origin resulting in much colder temperatures. Thus, the lower fecundity in the Fortune Bay sample is likely linked with an overall reduction in productivity in a cold water environment. Reduced productivity has been observed previously in the cold water habitats of le Fjord du Saguenay, Quebec (Couture 1971) and the Barents Sea (Berenboim 1982).

The sample taken east of Baffin Island showed relatively high fecundity in cold water (0.7°-1.8°C) compared with other cold water areas. Also, average size of females was larger than encountered elsewhere with largest females carrying clutches in excess of 4,300 eggs. This is similar to a situation in the Sea of Japan where female shrimp carried similar numbers of eggs as those (at comparable lengths) off Labrador. Again, greater sizes were attained and egg counts as high as 4,900 were encountered (Ito 1976). Growth and maturation are delayed in colder water (Allen 1959; Rasmussen 1969; Butler 1971) and shrimp in these two cold water environments likely live longer than conspecifics on the Labrador Shelf.

Dupouy et al. (1981) concluded that shrimp off Baffin Island spawned intermittently based on the high proportion of nonspawning females observed during a survey in 1979. If all females do not spawn annually, more time is available for growth. (Ovigerous females do not molt.) This can account for the larger sizes attained in the colder area. Failure to spawn annually reduces reproductive potential but is compensated to some degree by the large sizes females attain (larger females carry more eggs) and the apparently increased longevity.

Samples taken in 1982 in the Hudson Strait and North Labrador Sea came from waters of 0.6° and 0.5°C, respectively, but only data from the former were significantly different ($\alpha = 0.05$) from samples taken in the warmer Hopedale and Cartwright Channels. Data from Haynes and Wigley (1969) showed higher fecundity in warmer water (~5°C) of the Gulf of Maine where a 28 mm female can produce around 2,800 eggs compared with 1,900-2,000 in the Cartwright Channel (2°-3°C). In the Gulf of St. Lawrence, temperatures were similar to those in the Gulf of Maine but fecundity in 1970 (E. J. Sandeman[4] unpubl. data) was comparable with levels observed in the colder Labrador channels. Allen (1959) reported smaller shrimp and fewer eggs for *P. borealis* in the North Sea (~9°C) compared with the colder area off Southern Norway (7°C).

CONCLUSIONS

Fecundity of *Pandalus borealis* in the areas of the Northwest Atlantic considered in this study was generally lower than observed previously in the Gulf of Maine (Haynes and Wigley 1969) and off Southern Norway (Rasmussen 1953). Fecundity can vary seasonally, annually, and between areas, making conclusions based on such data difficult. Skúladóttir et al. (1978) concluded that fecundity does not seem to be a useful characteristic for distinguishing between populations unless it is certain that no egg loss or hatching has taken place. The results of the present study concur with these findings and those of Teigsmark (1983) which also showed that annual variation within areas also must be considered.

In some comparisons between areas, there appears to be reduced egg production in areas with low environmental temperature. In others, this is not at all apparent, especially at extremely cold and warm temperatures. Thus, there is no clear relationship between fecundity and environmental temperature, especially at the extremes of the range of temperature tolerance.

Squires (1968) described warm water areas as areas of high reproductive potential for shrimp and colder regions as areas of low reproductive potential. The cold water bays of Newfoundland and the eastern Hudson Strait fit into the latter category in terms of shrimp fecundity. Other cold water concentrations of shrimp appear to be better adapted such as those off Baffin Island, in the North Labrador Sea and Sea of Japan. In these cases, environmental conditions other than temperature (e.g., availability of nutrients) may be more important.

ACKNOWLEDGMENTS

We are grateful to the many technicians and casual employees who assisted in collecting the data over the years and performed the laborious task of counting the eggs. In this regard, the services of W. Edison are particularly appreciated. Assistance in the statistical analyses was provided by D. Stansbury.

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INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA FISHERY, 1973 THROUGH 1978

BRUCE E. WAHLEN[1]

ABSTRACT

Since the late 1950's, large numbers of dolphins have been killed incidentally in the yellowfin tuna purse seine fishery in the eastern tropical Pacific. Estimates of numbers of dolphins killed incidentally in this fishery from 1973 through 1978 were made previously using a stratified ratio estimator. Previous estimates were revised by reducing the number of strata and incorporating revisions in the data. Revised estimates of total mortality, which are consistently more precise than previous estimates, declined from about 100,000 dolphins per year from 1973 through 1976 to about 25,000 and 15,000 during 1977 and 1978. The decline in estimated mortality between 1976 and 1977 was primarily the result of a decline in the kill rate which coincided with a significant management action in late 1976. Other examples during the 1964 through 1982 period of such a temporal correspondence between a change in the number or distribution of dolphins killed and legal or management actions are discussed.

Since the late 1950's, tuna purse seine fishermen operating in the eastern tropical Pacific Ocean (ETP) have exploited several dolphin species—primarily spotted dolphins, *Stenella attenuata*, and spinner dolphins, *S. longirostris*, and also striped dolphins, *S. coeruleoalba*, and common dolphins, *Delphinus delphis*—to locate and catch yellowfin tuna, *Thunnus albacares*. Perrin (1969) described the process of deploying, or setting, the net around the tuna and dolphins, and then releasing the dolphins while retaining the tuna. During this process, however, large numbers of dolphins have been killed incidentally by becoming entangled in the purse seines (Smith 1983).

The U.S. Marine Mammal Protection Act of 1972 mandated the Secretary of Commerce to make periodic assessments of the condition of dolphin populations involved in this ETP fishery. As a result of a 1976 ruling by a U.S. District Court regarding regulations promulgated under the Act, the Federal Government established annual dolphin mortality limits for the U.S. registered fleet (Fox 1978). Estimates of annual dolphin mortality have been an integral component of periodic assessments (Smith 1983).

Estimates of cumulative dolphin mortality made throughout the year are used to monitor mortalities relative to the annual limits (Lo et al. 1982). When a particular limit is reached, regulations prohibit U.S. registered vessels from fishing on the affected populations for the remainder of the year. In October 1976, the National Marine Fisheries Service (NMFS) issued a prohibition notice for the first time (Federal Register 1976), but because of litigation the notice did not become effective until November 1976.

In recent years, researchers have published several estimates and revisions of estimates of dolphin mortality incidental to this fishery. For the period 1959-78, estimates have been made by Smith (1979[2]), Lo et al. (1982), Smith (1983), and Lo and Smith (1986); for the years 1979-83, see Allen and Goldsmith (1981, 1982), Lo et al. (1982), Hammond and Tsai (1983), Hammond (1984), and Hammond and Hall (1985).

Lo et al. (1982) suggested that previous estimates of dolphin mortality incidental to this fishery were based on a stratification scheme with an unnecessarily large number of strata. In this paper, I revise the 1973-78 estimates for U.S. registered purse seiners by reducing the number of strata and by incorporating revisions in the data.

DATA

Sample data were obtained from recorded observations of scientific observers who had been placed by the NMFS aboard selected U.S. registered tuna purse seine vessels fishing in the ETP. Data recorded by these observers included the type, date,

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.

[2] Smith, T. D. (editor). 1979. Report of the status of porpoise stocks workshop, La Jolla, Calif., 27-31 August 1979. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-41, 120 p.

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FISHERY BULLETIN: VOL. 84, NO. 3, 1986.

location, and estimated tuna catch of each set, and other information describing the fishing operation. For sets involving dolphins (dolphin sets), the observers collected additional data, including the number of dolphins killed by species.

In 1973, all sampled trips were arranged with vessel captains under a voluntary sampling program. Beginning in 1974, trips to be sampled were determined from a randomly ordered list of vessels. Which trips were actually sampled during 1974 and 1975 depended on several factors, including the cooperation of the captains. Because of uncertainties about the cooperation of the captains and the number of fishing trips that would be made in a year, observers were placed on vessels as soon as possible. Thus, before 1976, the planned number of sampled trips was frequently obtained in the first half of the year. The sampling process became more random starting in 1976, when participation in the sampling program became mandatory for captains making sets on dolphins.

I extracted independent information for the population of all fishing trips by U.S. registered tuna purse seiners in the ETP from the Inter-American Tropical Tuna Commission (IATTC) logbook data base. This data base contains abstracts of vessels' logbooks obtained by IATTC personnel. An individual entry in the logbook data base provides information about one or more sets, including number of sets, set type, date and location, estimated tuna catch by species, but not numbers of dolphins killed.

The logbook data are incomplete in that number of sets may be missing, set type may not be recorded, and information for some sets of a trip and for all sets of some trips may be omitted (Punsly 1983). To compensate for these omissions from the logbook data, Punsly (1983) estimated the total number of dolphin sets made by all U.S. and non-U.S. seiners in the ETP. He then modified this procedure to estimate the total number of dolphin sets made by U.S. seiners only (Table 1).

METHODS

I stratified the data to allow for potential differences in dolphin kills. If kills do indeed differ among strata, then a stratified estimator may be superior to an unstratified estimator in two respects. First, a stratified estimator will have a smaller standard error and thus be more precise. Second, if the sample data are unrepresentative of the population with respect to these strata, a stratified estimator will be less biased.

Therefore, estimates of incidental dolphin mortality by species or species grouping were computed using a stratified kill-per-set ratio estimator, following the general approach described by Lo et al. (1982). I excluded trips which made no dolphin sets and experimental-gear trips from the sample and the population. However, I added dolphin kills incidental to the experimental-gear trips as constants to the mortality estimates.

I stratified the dolphin set data by four factors used in previously published estimates: 1) year of the set, 2) fish-carrying capacity of the vessel, or simply vessel capacity, 3) period within year of the set, and 4) geographic location of the set. Vessel capacity was divided into two categories—small and large. The breakpoint between categories was determined by examining the cumulative distribution of sampled trips by capacity. Periods were defined to be quarters of the year, considering the results of Wahlen and Smith (1985). The ETP was divided into three geographic areas—North Inside, North Outside, and South (Fig. 1)—because mean kill (per set) after 1978 has been shown to differ among these areas.[3]

In previous estimates, the amount of tuna caught in the set was included as a stratification factor. However, Hammond and Tsai (1983) found that stratification by this factor made very little difference in their estimates. For that reason and to avoid possible overstratification, I omitted amount of tuna caught as a stratification factor.

I pooled dolphin set data over strata when it was determined that between-strata differences in mean kill were not statistically significant or that sample sizes were otherwise too small. I prorated the estimated numbers of dolphin sets made by U.S. seiners (Table 1) among the pooled strata according to pro-

TABLE 1.—Estimated number of dolphin sets made by U.S. purse seiners fishing in the eastern tropical Pacific, by year.[1]

Year	Number of dolphin sets
1973	8,341
1974	7,475
1975	7,902
1976	7,126
1977	7,239
1978	4,214

[1] Peterson, C. L. (editor). 1984. The quarterly report October-December 1983 of the Inter-American Tropical Tuna Commission. Inter-Am. Trop. Tuna Comm., c/o Scripps Inst. Oceanogr., La Jolla, CA 92093.

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[3] K.-T. Tsai, Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92093, pers. commun. December 1983.

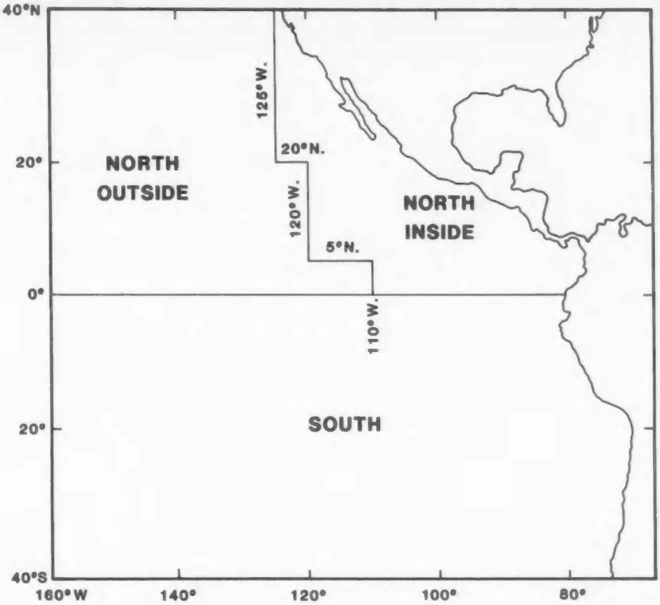

FIGURE 1.—The three areas of the eastern tropical Pacific used to stratify the data, bounded by lat. 40°N, long. 160°W, lat. 40°S, and the western coastline of the North and South American continents.

portions of known dolphin sets which were calculated from logbook data.

I tested for significant between-strata differences in mean total kill using analysis of variance (ANOVA) methods of BMDP programs P7D and P2V (Dixon 1983). Violation of the ANOVA assumption of equal cell variances may seriously distort significance probabilities in unbalanced models such as in this study (Glass et al. 1972). Because such distortion could be great, test results were considered to be inconclusive when significance probabilities were close to 0.05.

I was unable to test for the combined effect of all four stratification factors using the whole data set because data were sparse or unavailable in many of the 144 cells of the proposed four-factor stratification. Thus, ANOVA results for restricted subsets of the data containing adequate sample sizes were assumed to hold for subsets with inadequate sample sizes. To eliminate significant between-factor interactions, I tried logarithmic and power transformations of the dependent variable, total number of dolphins killed. When these transformations failed to eliminate the interactions, I partitioned the analysis into individual levels of the interacting variables.

When it was necessary to determine where the within-factor differences occurred, *t*-tests for differences between all pairs of cell means were made. Since I tested for differences between all pairs rather than between a few preselected pairs, a difference was considered significant if its significance probability was less than the quotient of 0.05 and the number of pairs. This Bonferroni adjustment to the significance level of each test assured a level of 0.05 simultaneously across all tests (Snedecor and Cochran 1980).

I computed *t*-values for pairwise differences using separate rather than pooled variance estimates because the cell variances were unequal according to Levene's test; this test was selected because it is more robust under nonnormality than either the common *F*-ratio or Bartlett's test (Brown and Forsythe 1974). Degrees of freedom were calculated with Satterthwaite's approximation, so that significance probabilities could be obtained from an ordinary *t*-distribution (Snedecor and Cochran 1980).

TABLE 2.—Cumulative distributions of number of sampled U.S. purse seine trips, by vessel capacity (tons) for the years 1973-78, with relative frequencies (percents) in parentheses.

Vessel capacity (tons)	Year					
	1973	1974	1975	1976	1977	1978
<200	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<300	0 (0)	1 (3)	1 (3)	0 (0)	0 (0)	0 (0)
<400	1 (4)	3 (8)	2 (7)	3 (7)	0 (0)	0 (0)
<600	5 (22)	9 (24)	5 (17)	11 (24)	15 (15)	8 (8)
<800	15 (65)	15 (41)	8 (28)	20 (43)	34 (35)	27 (26)
<1,000	16 (70)	20 (54)	16 (55)	24 (52)	39 (40)	33 (32)
<1,200	20 (87)	30 (81)	26 (90)	34 (74)	70 (71)	67 (66)
Total	23 (100)	37 (100)	29 (100)	46 (100)	98 (100)	102 (100)

RESULTS

Setting the breakpoint between small and large vessel capacities at 600 tons (or lower) or at 1,200 tons would, in each case, create small and large vessel categories with severely unbalanced sample sizes (Table 2). The percent of sampled vessels with capacity <1,000 tons was more stable over years than the percent of sampled vessels <800 tons, especially from 1973 through 1976. Therefore, the breakpoint between vessel categories was set at 1,000 tons.

Because of data sparseness, particularly in the North Outside and South areas (Table 3), I made three multiway ANOVA tests restricted to subsets of the whole data set: 1) two-way test of year and vessel capacity, restricted to the North Inside area and the second quarter, 2) three-way test of year, quarter, and vessel capacity, restricted to the North Inside area and the first two quarters during 1973 through 1976, and 3) four-way test, restricted to the North Inside and North Outside areas, and the

TABLE 3.—Number of dolphin sets made during sampled trips, by year, vessel capacity (tons), quarter of the year, and area.

Year	Vessel capacity (tons)	Quarter	Area			
			North Inside	North Outside	South	Total
1973	<1,000	1	325	0	9	334
		2	167	47	0	214
		3	0	0	0	0
		4	0	0	0	0
		Total	492	47	9	548
	≥1,000	1	116	0	5	121
		2	43	2	0	45
		3	0	0	0	0
		4	0	0	0	0
		Total	159	2	5	166
1974	<1,000	1	459	0	0	459
		2	88	0	0	88
		3	0	6	0	6
		4	0	0	0	0
		Total	547	6	0	553
	≥1,000	1	362	0	0	362
		2	57	0	0	57
		3	31	12	0	43
		4	0	0	0	0
		Total	450	12	0	462
1975	<1,000	1	404	0	3	407
		2	106	0	4	110
		3	0	0	0	0
		4	0	0	0	0
		Total	510	0	7	517
	≥1,000	1	268	0	0	268
		2	111	0	5	116
		3	47	0	0	47
		4	0	0	0	0
		Total	426	0	5	431
1976	<1,000	1	155	0	0	155
		2	41	27	0	68
		3	18	71	0	89
		4	20	13	4	37
		Total	234	111	4	349
	≥1,000	1	129	0	118	247
		2	42	0	0	42
		3	17	80	1	98
		4	16	6	0	22
		Total	204	86	119	409
1977	<1,000	1	3	0	1	4
		2	239	67	0	306
		3	433	134	0	567
		4	53	0	0	53
		Total	728	201	1	930
	≥1,000	1	0	0	2	2
		2	563	86	16	665
		3	1,034	218	23	1,275
		4	356	30	31	417
		Total	1,953	334	72	2,359
1978	<1,000	1	170	0	13	183
		2	75	50	0	125
		3	86	138	0	224
		4	59	6	0	65
		Total	390	194	13	597
	≥1,000	1	320	0	52	372
		2	117	77	1	195
		3	104	255	2	361
		4	165	8	15	188
		Total	706	340	70	1,116
Total			6,799	1,333	305	8,437

second and third quarters during 1977 and 1978. Additionally, pairwise *t*-tests were made to isolate annual and quarter differences detected by the above tests.

Tests for Year Differences

Sample statistics of mean kill by year and vessel capacity (Test 1) revealed an unbalanced design and suggested that cell variances were related to cell means (Table 4). For each of several transformations of total kill, neither the interaction between vessel capacity and year nor the difference between vessel capacities was significant, but the difference among years was significant.

To determine where the yearly differences occurred, the data were pooled over vessel capacity so that *t*-tests for differences between each pair of yearly means could be made. The resulting one-way classification by year was unbalanced and characterized by significantly different cell variances ($P < 0.001$), and suggested that the means from 1973 through 1976 were larger than the means from 1977 and 1978 (Table 4).

TABLE 4.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by year and vessel capacity (tons) for all sets made in the North Inside area during quarter two. Significance probabilities (P) obtained for 2-way ANOVA's on transformed values of total kill: interaction ($P \geqslant 0.1180$), year ($P < 0.001$), and vessel capacity ($P \geqslant 0.7851$).

Vessel capacity (tons)	Statistic	Year					
		1973	1974	1975	1976	1977	1978
<1,000	$\bar{k}$	8.62	6.20	16.33	8.58	3.08	2.35
	s	18.84	10.94	40.73	20.08	11.64	7.34
	d	167	88	106	41	239	75
⩾1,000	$\bar{k}$	11.49	5.25	8.79	14.57	2.53	1.18
	s	25.96	14.08	17.43	32.44	7.84	3.31
	d	43	57	111	42	563	117
Pooled	$\bar{k}$	9.21	5.83	12.47	11.61	2.69	1.64
	s	20.46	12.23	31.23	27.05	9.13	5.28
	d	210	145	217	83	802	192

TABLE 5.—Matrix of significance probabilities associated with *t*-tests for differences between pairs of annual means of total number of dolphins killed. Significant values, required by the Bonferroni adjustment to be <0.0033, are indicated by "*", and nearly significant values are indicated by "+". Data are from sampled dolphin sets made during quarter two in the North Inside area.

Year	Year				
	1974	1975	1976	1977	1978
1973	0.0526	0.2007	0.4659	0.0000^{*}	0.0000^{*}
1974		0.0050	0.0681	0.0037^{+}	0.0002^{*}
1975			0.8139	0.0000^{*}	0.0000^{*}
1976				0.0037^{+}	0.0013^{*}
1977					0.0344

Results from pairwise *t*-tests indicated that means were not significantly different within each of the two periods from 1973 through 1976 and from 1977 through 1978 (Table 5). However, each of the means from 1973 through 1976 was significantly different (or nearly so) from each of the means from 1977 and 1978 (Table 5). Based on these results, I divided the data into two periods, 1973 through 1976 and 1977 through 1978, for further tests within each period.

Tests for Differences Within the 1973-76 Period

The three-way ANOVA table by year, quarter, and vessel capacity (Test 2) was unbalanced and suggested that cell variances were unequal (Table 6). Furthermore, no between-factor interactions were significant. The test for year differences was inconclusive; however, there is evidence for a year effect within only one cell (1976, quarter 1, small vessels), and there is no consistent yearly pattern of means within rows of the table. Therefore, I concluded that annual means during 1973-76 were not significantly different and, hence, I pooled over years within this period. I also pooled over vessel capacity since it was not a significant effect during these years.

Before 1976, sample data were unrepresentative of quarter and area, since nearly all data were obtained from trips made during the first half of the year and, thus, within the North Inside area. Data sparseness in the North Outside and South areas,

TABLE 6.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by year, quarter, and vessel capacity (tons) for all sets made in the North Inside area during the first two quarters of 1973-76. Significance probabilities (P) obtained for a 3-way ANOVA on total kill: interactions ($P \geqslant 0.1374$), year ($P = 0.0534$), quarter ($P = 0.0501$), and vessel capacity ($P = 0.8219$).

Vessel capacity (tons)	Quarter	Statistic	Year			
			1973	1974	1975	1976
<1,000	1	$\bar{k}$	23.15	14.10	16.45	3.47
		s	69.70	40.39	47.31	8.12
		d	325	459	404	155
	2	$\bar{k}$	8.62	6.20	16.33	8.59
		s	18.84	10.94	40.73	20.08
		d	167	88	106	41
⩾1,000	1	$\bar{k}$	15.75	11.23	15.45	10.86
		s	27.64	24.85	34.37	24.35
		d	116	362	268	129
	2	$\bar{k}$	11.49	5.25	8.79	14.57
		s	25.95	14.08	17.43	32.44
		d	43	57	111	42

resulting from the unrepresentative areal sample, precluded testing for an area effect during the 1973-76 period (Table 3); however, after 1978 mean kills were shown to differ among the three areas, as noted earlier. Therefore, to minimize the amount of bias which might be introduced into the estimates from a sample which was unrepresentative of area, I retained the three-area stratification.

Small sample sizes during 1973-76 dictated pooling over all quarters within both the North Outside and South areas and over quarters 3 and 4 within the North Inside area (Table 3). The test result for quarter 1 and 2 differences in the North Inside area was inconclusive (Table 6). Based on bias considerations similar to those above, I did not pool data from quarters 1 and 2 in the North Inside area in case their means did indeed differ.

After pooling over year, vessel capacity, and quarter as indicated above, five strata remained for the 1973-76 data: 1) North Inside, quarter 1, 2) North Inside, quarter 2, 3) North Inside, quarters 3 and 4 pooled, 4) North Outside, all quarters pooled, and 5) South, all quarters pooled.

Tests for Differences Within the 1977-78 Period

Interpretation of the four-way ANOVA (Test 3), restricted by data sparseness to the North Inside and North Outside areas during the second and third quarters of 1977-78 (Table 3), was complicated by significant interaction between quarters and each of the other three factors ($P \leq 0.0159$, for total kill and all transformations of total kill). Therefore, the four-way table was partitioned into two, three-way tables, one for each level of quarter (Tables 7, 8), and decisions about between-strata differences during these years were based on results obtained separately for each quarter.

For second quarter data, interactions were not significant (Table 7). However, for third quarter data, interaction between year and vessel capacity was significant ($P < 0.001$) primarily because of the two large means recorded in the North Inside and North Outside areas by small vessels during 1978 (Table 8). Omitting the data from one extraordinarily large kill set in each of these two cells reduces their means from 11.27 to 4.68 for the North Inside and from 9.77 to 5.46 for the North Outside.

Results from the second and third quarter data were inconsistent for both year and vessel capacity. Neither effect was significant during the second quarter (Table 7), but during the third quarter (Table 8) the large means in the two cells noted above provided some evidence of both a year and vessel capacity effect. Since the evidence for both a year and vessel capacity effect was confined to two, third quarter cells whose means were each strongly influenced by only one set, I concluded that year and vessel capacity were not significant effects during 1977-78. Hence, I pooled over year and vessel capacity within this period. The evidence regarding an area effect during 1977-78 was also inconsistent between quarters (Tables 7, 8); however, I retained area as a stratification factor since it was shown to be significant after 1978.

Beginning in 1976 when the sampling program became mandatory the sample data became more representative of quarter. Thus, for the 1977-78 data, bias considerations were of lesser importance

TABLE 7.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by area, vessel capacity (tons), and year for all sets made in the North Inside and North Outside areas during quarter two of 1977-78. Significance probabilities (P) obtained for a 3-way ANOVA on total kill: interactions ($P \geq 0.2095$), area ($P = 0.0060$), vessel capacity ($P = 0.8857$), and year ($P = 0.6050$).

Year	Vessel capacity (tons)	Statistic	Area	
			North Inside	North Outside
1977	<1,000	$\bar{k}$	3.08	2.94
		s	11.64	8.68
		d	239	67
	≥1,000	$\bar{k}$	2.53	5.66
		s	7.84	13.82
		d	563	86
1978	<1,000	$\bar{k}$	2.35	4.82
		s	7.34	16.00
		d	75	50
	≥1,000	$\bar{k}$	1.18	4.26
		s	3.31	21.19
		d	117	77

TABLE 8.—Mean of total number of dolphins killed ($\bar{k}$), standard deviation (s), and number of dolphin sets (d) for sampled trips, by area, vessel capacity (tons), and year for all sets made in the North Inside and North Outside areas during quarter three of 1977-78.

Year	Vessel capacity (tons)	Statistic	Area	
			North Inside	North Outside
1977	<1,000	$\bar{k}$	2.08	2.33
		s	5.72	7.92
		d	433	134
	≥1,000	$\bar{k}$	2.85	2.89
		s	9.81	6.45
		d	1034	218
1978	<1,000	$\bar{k}$	11.27	9.77
		s	61.74	52.52
		d	86	138
	≥1,000	$\bar{k}$	2.00	2.81
		s	4.34	10.97
		d	104	255

in stratification decisions than for the 1973-76 data. The four-way test on 1977-78 data (Test 3) was not helpful in resolving the question of quarter differences because of the interactions between quarter and each of the other three factors. However, pairwise *t*-tests for differences between quarterly means in the North Inside area during 1977-78, pooled over year and vessel capacity, detected no significant quarter differences (Table 9). Based on that result, I pooled over all quarters in the North Inside and North Outside areas. Finally, I pooled over all quarters in the South area because of the small sample sizes (Table 3).

TABLE 9.—Matrix of significance probabilities associated with *t*-tests for differences between pairs of quarterly means of total number of dolphins killed. No significant values, required by the Bonferroni adjustment to be <0.0083, were attained. Data are from sampled dolphin sets made in the North Inside area from 1977 through 1978.

	Quarter		
Quarter	2	3	4
1	0.7062	0.2417	0.0684
2		0.2623	0.0730
3			0.2831

Thus, after pooling over year, vessel capacity, and quarter as indicated above, only three strata remained for the 1977-78 data: 1) North Inside, 2) North Outside, and 3) South.

Estimates

I obtained annual estimates of the total number of dolphins killed by summing estimates for each of three or five strata, depending on the year. Estimates for a stratum were computed as the product of (a) total number of dolphin sets (Table 10) and (b) the corresponding total kill-per-set ratio (Table 11), increased by (c) the observed total number of dolphins killed during experimental-gear trips (Table

TABLE 10.—Estimated number of dolphin sets (D) and number of trips (N) for the population of trips, by year within strata.

		North Inside						
Year	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South	Total
1973	D	3,203	1,670	501		2,591	330	8,295
	N	172	104	69		117	34	
1974	D	3,486	1,176	242		2,453	12	7,369
	N	126	92	38		93	4	
1975	D	3,069	1,749	434		2,495	53	7,800
	N	119	96	40		96	23	
1976	D	1,618	1,520	716		2,001	729	6,584
	N	127	98	92		90	76	
1977	D				5,722	1,128	252	7,102
	N				186	76	37	
1978	D				2,811	1,153	162	4,126
	N				206	58	27	

TABLE 11.—By-trip means of total number of dolphins killed ($\bar{k}$) and of number of dolphin sets ($\bar{d}$), total kill-per-set ratio ($\hat{R}$), estimated standard error of the total kill-per-set ratio (s), and number of sampled trips (n), by strata.

		North Inside					
Years	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South
1973-76	$\bar{k}$	354.51	157.32	155.50		265.06	239.85
	$\bar{d}$	24.11	15.98	9.31		16.50	7.45
	$\hat{R}$	14.70	9.85	16.70		16.06	32.19
	s	1.19	1.15	4.38		4.21	4.17
	n	92	41	16		16	20
1977-78	$\bar{k}$				58.66	57.55	22.12
	$\bar{d}$				19.88	13.71	4.73
	$\hat{R}$				2.95	4.20	4.68
	s				0.23	0.51	1.03
	n				190	78	33

12). For example, the total estimated kill for 1977 (Table 13) was obtained as a sum of estimates of the total for three strata as [(5,722)(2.95) + 175] + [(1,128)(4.20) + 15] + [(252)(4.68) + 0]. Estimates for each species or species grouping were obtained in the same manner as estimates of the total, except that values for the species or species grouping were substituted for the totals in (b) and (c) above.

Similarly, I estimated the variance of the number of dolphins killed during any year by summing variance estimates for each stratum. The estimated variance of total kill for a stratum was computed

TABLE 12.—Total number of dolphins killed (*k*), number of dolphin sets (*d*), and number of experimental-gear trips (*n*), by year within strata. These data were excluded from all sample and population statistics.

		North Inside						
Year	Statistic	Quarter 1	Quarter 2	Quarters 3 & 4	Total	North Outside	South	Total
1973	*k*	0	0	513		0	0	513
	d	0	0	46		0	0	46
	n	0	0	2		0	0	
1974	*k*	0	0	497		192	0	689
	d	0	0	70		36	0	106
	n	0	0	2		1	0	
1975	*k*	0	0	512		271	0	783
	d	0	0	76		26	0	102
	n	0	0	2		1	0	
1976	*k*	139	1,400	111		1,886	547	4,083
	d	35	256	92		153	6	542
	n	2	16	7		5	2	
1977	*k*				175	15	0	190
	d				129	8	0	137
	n				4	2	0	
1978	*k*				226	27	0	253
	d				77	11	0	88
	n				6	2	0	

TABLE 13.—Estimates of dolphin mortality incidental to U.S. purse seiners, by species grouping and year, with coefficients of variation in parentheses.

	Year					
Species grouping	1973	1974	1975	1976	1977	1978
Spotted	70,000 (0.12)	61,000 (0.13)	63,000 (0.13)	61,000 (0.11)	14,000 (0.08)	9,000 (0.08)
Spinner						
Eastern[1]	12,000 (0.16)	11,000 (0.11)	11,600 (0.11)	9,500 (0.12)	1,300 (0.12)	700 (0.11)
Whitebelly	20,000 (0.17)	16,000 (0.19)	17,000 (0.19)	19,000 (0.15)	3,600 (0.11)	2,300 (0.10)
Unidentified	8,700 (0.24)	7,600 (0.26)	7,700 (0.25)	7,500 (0.25)	60 (0.18)	40 (0.17)
Total	41,000	35,000	36,000	36,000	5,000	3,000
Common	8,500 (0.22)	7,000 (0.25)	8,300 (0.22)	6,600 (0.20)	3,000 (0.23)	1,500 (0.24)
Striped	640 (0.30)	380 (0.34)	500 (0.35)	800 (0.33)	200 (0.26)	130 (0.24)
Unidentified	5,000 (0.19)	3,700 (0.20)	4,000 (0.19)	5,400 (0.26)	450 (0.12)	300 (0.12)
Other	180 (0.45)	90 (0.26)	100 (0.26)	280 (0.64)	180 (0.22)	100 (0.26)
Total[2]	125,000 (0.10)	107,000 (0.10)	112,000 (0.10)	110,000 (0.09)	23,000 (0.06)	14,000 (0.06)

[1] May include small number of Costa Rican spinner dolphins.

[2] Sum of estimated kills over species grouping not exactly equal to total estimated kill because of rounding error.

as the square of the product of (a) the number of dolphin sets[4] (Table 10) and (b) the corresponding estimated standard error of the total kill-per-set ratio (Table 11). I computed the estimated stratum variance for each species or species grouping, substituting values for the species or species grouping for the total in (b) above. I estimated the standard errors (Table 11) using mean number of dolphin sets per trip calculated from the sample rather than from the population (Lo et al. 1982).

My annual estimates of the total number of dolphins killed incidentally in the U.S. purse seine fishery of the ETP ranged from a maximum of 125,000 dolphins in 1973 to a minimum of 14,000 dolphins in 1978, with coefficients of variation (CV) no greater than 10% (Table 13). The estimated mortalities of the two species most often exploited, spotted and spinner dolphins, together accounted for about 80-90% of each annual total.

DISCUSSION AND CONCLUSIONS

The kill-per-set ratio, or mean kill, declined from 15 dolphins/set during the 1973-76 period to 3 dolphins/set during the 1977-78 period (Table 11, pooled over quarter and area). Many changes affecting dolphin kill were made during these periods, including improvements in fishing gear and dolphin-release procedures and introduction of federal regulations. The change in mean kill between 1973-76 and 1977-78 coincided with the first NMFS notice in late 1976 prohibiting fishing on dolphins for the remainder of the year. This one example of a correspondence between a change in the number or distribution of dolphins killed during purse seine sets and an identifiable legal or management action is not necessarily indicative of a cause and effect relationship. There are, however, two other examples of such a temporal correspondence present in the data from 1964 through 1982.

In the second example, the data prior to 1973, while sparse, suggest that the mean kill was substantially higher than during the 1973-76 period. Lo and Smith (1986) reported a mean kill of 46 dolphins/set based on 1964 through 1972 data, pooled over vessel capacity and catch of tuna. They found no consistent differences in annual mean kill during that period. The decline in the mean from 46 dolphins/set during the 1964-72 period to 15 dolphins/set during the 1973-76 period coincided with the passage of the Marine Mammal Protection Act in late 1972.

In the third example, Wahlen and Smith (1985) demonstrated a difference between the two periods from 1979 through March 1981 and from April 1981 through 1982 in the frequency distributions of number of dolphins killed during purse seine sets. While the difference in mean kill during these two periods was not significant, the percent of dolphin sets in which no dolphins were killed (zero-kill sets) decreased significantly. This decrease coincided with a court order in March 1981 which prohibited using data collected by NMFS observers to monitor compliance of vessel captains with dolphin-release procedures.

These three examples suggest that significant legal or management actions can affect kill rates, measured by the kill-per-set ratio or by the percent of zero-kill sets. Furthermore, such effects on the kill-per-set rate are reflected in the series of estimates of total numbers of dolphins killed presented here. For example, between 1976 and 1977 the number of dolphin sets increased slightly (Table 10), yet total estimated mortality decreased by nearly 80% (Table 13), due primarily to the significantly lower kill rate after 1976. The further decline in estimated mortality to 14,000 dolphins in 1978 reflects both the lower kill rate and a decline in the number of dolphin sets. Thus, the decrease in the kill rate following the first enforcement of dolphin kill limits in 1976 is reflected in the decrease in the estimates of total mortality after 1976.

My estimates of total annual dolphin mortality in U.S. purse seine fishing from 1973 through 1978 (Table 13) are lower, except for 1976, and more precise than those in the Status of Porpoise Stocks Workshop Report (SOPS) (Table 14). However, for each year except 1973, my estimated total is contained inside an approximate 95% confidence interval around the estimated total ($\hat{T}$) in SOPS, where the confidence interval is computed as $\hat{T} \pm 2 \cdot \mathrm{CV} \cdot \hat{T}$. Thus, the differences between my point estimates and those in SOPS are small when the imprecision (large CV) of the SOPS estimates is considered.

The lower precision of the SOPS estimates may be due to overstratification because of a concern that the sample might not be representative of the population, particularly during the 1973-75 period. Thus, in order to minimize bias, a large number of strata (32 per year) were defined. Tests for between-strata differences in mean kill were not made, but strata were pooled to the degree that each pooled stratum contained some sample data. However, even after pooling, some strata during the years 1973-76

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[4] Numbers of dolphin sets were treated as constants since no variances were provided for these estimated quantities. Therefore, my variances of estimated mortality are underestimated to an unknown, though likely small, degree.

TABLE 14.—Estimates of dolphin mortality incidental to U.S. purse seiners, by species and year, from Status of Porpoise Stocks Workshop Report (Smith text footnote 2). Coefficients of variation of totals in parentheses.

Species	Year 1973	1974	1975	1976	1977	1978
Spotted	114,000	75,000	84,000	57,000	12,000	13,000
Spinner	65,000	62,000	70,000	39,000	5,000	4,400
Common	18,000	3,000	2,300	5,400	6,600	1,000
Striped	40	140	900	2,000	100	250
Unidentified[1]	0	0	0	0	0	0
Other	0	80	160	690	80	50
Total[2]	197,000 (0.17)	140,000 (0.41)	157,000 (0.17)	104,000 (0.13)	24,000 (0.15)	19,000 (0.20)

[1] Kills of unidentified dolphins prorated among known species.

[2] Sum of estimated kills over species not exactly equal to total estimated kill because of rounding error.

contained only one dolphin set. Such small sample sizes within some strata account for the lower precision of the SOPS estimates relative to my estimates.

While the differences between my point estimates and those in SOPS are small in a statistical sense, my estimates are consistently lower except for 1976. However, these new estimates are to be preferred on methodological grounds. I tested for statistically significant between-strata differences in mean kill and pooled over strata when significant differences were not detected or when sample sizes were otherwise too small. Pooling of the data produced estimates which were more precise than the SOPS estimates because it resulted in fewer strata with larger sample sizes. However, to minimize the possibility of introducing bias into the estimates during the 1973-76 period, when the sample was unrepresentative of area and quarter, I did not pool over area and I pooled over quarter only in the event of small sample sizes.

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DISTRIBUTION AND REPRODUCTIVE BIOLOGY OF THE GOLDEN KING CRAB, *LITHODES AEQUISPINA*, IN THE EASTERN BERING SEA

DAVID A. SOMERTON[1] AND ROBERT S. OTTO[2]

ABSTRACT

The golden king crab is a large anomuran that supports a new, rapidly expanding fishery in the eastern Bering Sea and Aleutian Islands. Based on size, sex, and abundance data collected by U.S. observers aboard foreign trawlers and by National Marine Fisheries Service personnel aboard research vessels, we examined latitudinal and depth variation in mean size (carapace length), size at maturity, weight at size, and relative abundance. Mean size decreases by 6.2 mm for males and 4.6 mm for females with each 1 degree increase in latitude. Size at maturity decreases with increasing latitude from 130 mm for males and 111 mm for females in the southern area to 92 mm and 98 mm in the northern area. These decreases may be due to a temperature induced decrease in growth rate. Weight at size increases by 10% from the southern to the northern area owing to a latitudinal change in body shape. Mean size and relative abundance of both sexes increase with a decrease in depth, suggesting that an onshore ontogenetic migration occurs and that adult males migrate into somewhat shallower water than adult females. Fecundity (number of uneyed embryos) of northern females increases with size according to $-24815 + 323$ CL, where CL is carapace length. This relationship changes with latitude and southern females carry about 1,330 fewer eggs than equal-sized northern females. Mean length of uneyed eggs is 2.2 mm. Based on the lack of a clear seasonal change in the occurrence of eyed and uneyed clutches, golden king crab appear to have protracted, or perhaps year-round, breeding.

The golden king crab, *Lithodes aequispina*, is a large anomuran that inhabits the upper continental slope from southern British Columbia, Canada, northward to the Bering Sea and westward to Suruga Bay, Japan (Butler and Hart 1962; Suzuki and Sawada 1978). Although similar in size to red king crab, *Paralithodes camtschatica*, and blue king crab, *P. platypus*, the traditional species harvested by Alaskan crab fisheries, golden king crab have not been intensively harvested because they live in deeper water than red and blue king crabs and are therefore more difficult and expensive to capture (McNair 1983). Since 1980, however, precipitous declines in abundance of red and blue king crabs have stimulated growth of directed fisheries for golden king crab. These fisheries expanded rapidly in the eastern Bering Sea and Aleutian Islands, and between 1981 and 1983 the catch of golden king crab increased from 50 t to 4900 t or 44% of the total king crab catch from these areas.

The fisheries for golden king crab have been managed according to regulations designed for red and blue king crabs (Alaska Department of Fish and Game 1983; Miller 1976) because little biological information was available to establish more specific regulations. Although golden king crab have been studied before, published reports either concern Asian stocks (Hiramoto and Sato 1970; Suzuki and Sawada 1978; Rodin 1970) or are restricted to taxonomy (Benedict 1895; Makarov 1938), distribution (Butler and Hart 1962; Slizkin 1974), or early life history (Haynes 1981).

In 1981, the National Marine Fisheries Service (NMFS) began collecting biological data on golden king crab necessary for establishing minimum size limits and fishing seasons. We summarize these data here, focusing our attention on latitudinal and depth gradients in mean size, size at maturity, weight at size, and sex ratio as well as various aspects of the reproductive biology. We then examine the management implications of our findings.

MATERIALS AND METHODS

Data Sources

Golden king crab were sampled by NMFS re-

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[1] Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA; present address: Southwest Fisheries Center Hawaii Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

[2] Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

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search personnel on stock assessment and tagging cruises and by NMFS observers aboard foreign fishing vessels. In the following we distinguish between survey data and observer data because the sampling designs differed considerably. In both cases, however, crabs were measured with calipers to the nearest millimeter according to the descriptions in Wallace et al. (1949).

TABLE 1.—Inclusive dates, latitude and depth ranges, number of crabs sampled and type of sampling gear are shown for each of the 10 golden king crab research cruises conducted by the National Marine Fisheries Service.

Year	Dates	Latitude (degrees *N*)	Depth (m)	Number males	females	Gear
1981	2/12-2/23	54.4-55.1	346-472	4	6	trawl
1982	7/12-8/4	58.3-60.9	168-849	292	341	trawl
1983	1/31-2/8	52.3-52.5	183-366	188	123	pot
	2/22-2/24	54.4-55.7	362-461	24	17	trawl
	5/9-5/10	56.0-56.1	365-421	288	1,114	pot
	5/12-5/15	57.8-58.5	329-365	489	1,753	pot
	7/8-7/10	57.7-57.7	347-365	1,073	741	pot
	7/14-7/18	55.9-56.3	311-384	1,285	1,012	pot
	10/2-10/4	56.2-56.2	347-365	596	1,035	pot
	11/15-11/21	52.4-52.6	110-283	376	404	pot

Survey Data

From 1981 to 1983, NMFS conducted 10 survey cruises sampling the eastern Bering Sea population of golden king crab with either bottom trawls or commercial king crab pots (Table 1). All crabs were measured for carapace length, and females were classified into one of four categories of reproductive condition:

1) Non-ovigerous - no embryos or empty egg cases attached to the pleopod setae.
2) uneyed embryos - embryos without conspicuous dark eyes.
3) eyed embryos - embryos with dark eyes.
4) empty egg cases - empty egg cases and funiculi attached to the pleopod setae.

When opportunity occurred, one or more of the following were also collected:

1) height of the right chela of males (excluding males with partially regenerated right chela).

2) Total wet body weight of males, measured to the nearest gram on a triple beam balance or to the nearest 5 g on a handheld spring scale (excluding males with damaged exoskeletons or missing appendages).

3) egg masses from females (stored in Formalin[3] diluted to 10% with seawater).

Observer Data

Golden king crab, like most of the other large Alaskan crabs, is classified as a prohibited species and, as such, may not be retained if captured by foreign fisheries. Because of this status, NMFS fishery observers routinely record the carapace length, sex, and number of golden king crab that are incidentally caught by foreign vessels during their normal fishing operations for other species (Nelson et al. 1981). To delineate the distribution of golden king crab in the eastern Bering Sea, we chose to examine the 1981 and 1982 observer data obtained from Japanese small stern trawlers that fish for turbot (*Reinhardtius hippoglossoides*) because 1) these vessels use trawls designed to remain in direct contact with the bottom and are therefore likely to catch crabs, 2) these vessels operate year-round along nearly the entire length of the continental slope of the eastern Bering Sea, and 3) turbot have a depth distribution similar to that of golden king crab. Although these data are not necessarily a random sample of the golden king crab population, they are the most extensive data available and include samples from the entire depth range of golden king crab during all four seasons. The number of crabs measured and the number of trawl hauls sampled are summarized by year, month, latitude, and depth (Table 2). Due to a lack of Japanese fishing effort for turbot, observer data were unavailable for areas south of lat. 54°15′N.

Both survey and observer data, in some instances, were partitioned into three latitudinal strata or subareas (Fig. 1): northern (north of lat. 58°30′N), central (between lat. 58°30′N and 54°15′N), southern (south of lat. 54°15′N and east of long. 173°00′W), which correspond approximately to the crab management districts used by the Alaska Department of Fish and Game. In addition, the observer data were partitioned into two depth strata separated at the approximate median depth (500 m) of the samples (nearly the entire depth range of golden king crab is bounded by the 200 m and 1,000 m isobaths).

Methods of Analysis

Size-frequency distributions by sex were constructed from the combined 1981 and 1982 observer

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Number of trawl hauls sampled (excluding hauls without crabs) and number of crabs sexed and measured by U.S. observers aboard Japanese small trawlers within the study area during 1981 and 1982. Data are summarized by depth, latitude and month.

	1981		1982	
	Hauls	Crabs	Hauls	Crabs
Depth (m)				
100	0	0	3	3
200	7	81	23	86
300	30	323	33	848
400	217	2,475	339	3,551
500	456	6,885	548	4,380
600	201	2,065	192	1,112
700	16	97	27	81
800	6	24	1	2
900	2	13	0	0
1,000	1	6	0	0
Latitude (degrees N)				
53	12	18	0	0
54	7	135	132	678
55	34	455	43	184
56	165	1,582	163	879
57	59	376	75	552
58	284	3,936	151	899
59	175	2,995	166	2,019
60	200	2,472	436	4,852
Month				
1	18	55	19	125
2	65	443	19	79
3	75	977	66	528
4	114	1,688	41	73
5	104	1,398	102	332
6	112	2,027	136	1,681
7	72	1,528	75	306
8	89	1,121	124	1,215
9	106	927	192	992
10	99	814	194	2,436
11	68	931	150	1,654
12	14	60	48	654
Total	936	11,969	1,166	10,063

data for each of the two depth strata within the northern and central subareas to help illustrate depth and latitude trends in the size distributions (see Figure 2). Potential bias because of the variation of fishing effort with depth was minimized by first partitioning the data into 100 m depth intervals. Within each depth interval, a size-frequency distribution and an average catch per hour (CPH) were calculated. Size-frequency distributions, weighted by the appropriate mean CPH, were then summed over all 100 m depth intervals within each of the two depth strata.

Variations in mean size, CPH, and proportion male with latitude and depth were also examined using multiple regression. Two normalizing transformations were used: 1) CPH was transformed to the natural log scale and 2) proportion male was transformed to the arcsine-square root scale after replacing 0 with $0.25/N$ and 1 with $(N - 0.25)/N$, where N is the number of crabs within each trawl haul (Bartlett 1947).

Egg size was estimated by randomly selecting 10 eggs from each preserved egg mass and measuring their maximum lengths (eggs are oval) to the nearest 0.1 mm with an ocular micrometer. The remainder of each egg mass was air dried and, after separating the eggs from the pleopods and setae, weighed to the nearest 0.1 mg. Two subsamples of about 200 eggs each were randomly selected from each dried egg mass and then weighed and counted. Fecundity was then estimated by dividing the total weight of an egg mass by the average of the two estimates of individual egg weight that were obtained from that egg mass.

Male size at maturity was estimated from the allometric growth of the right chela. When king crab chela measurements are plotted against carapace measurements on log-log axes, the data conform to two straight lines that intersect at the average carapace length at maturity (see Figure 3) (Somerton 1980; Somerton and MacIntosh 1983). To estimate this size, we used the computer method described in Somerton and MacIntosh (1983) which fits a pair of intersecting straight lines by iteratively varying the carapace length at the intersection point until the residual sum of squares about the lines is minimized. Variance of the male size at maturity was estimated using a computer technique known as bootstrapping (Efron and Gong 1983). In our application, the method consisted of randomly choosing, with replacement, 50 subsamples equal in size to the original data set. For each subsample, the size at maturity was estimated by fitting the two line model. Variance of the estimated size at maturity was then computed as the variance among the 50 independent estimates.

Although we attempted to detect and exclude partially regenerated chelae in the field, we were not always successful. Measurements from partially regenerated chelae can increase the variance of estimates of male size at maturity; therefore, these measurements were removed from the data set before analysis using a sequential outlier elimination technique described in Somerton and MacIntosh (1983).

Golden king crab females were considered to be mature, if they had eggs or empty egg cases attached to the pleopod setae. Although we are not certain that this is always true, for red and blue king crabs, adult females extrude eggs soon after every molt and the empty egg cases remain attached to the pleopod setae until the next molt (Somerton and MacIntosh 1985).

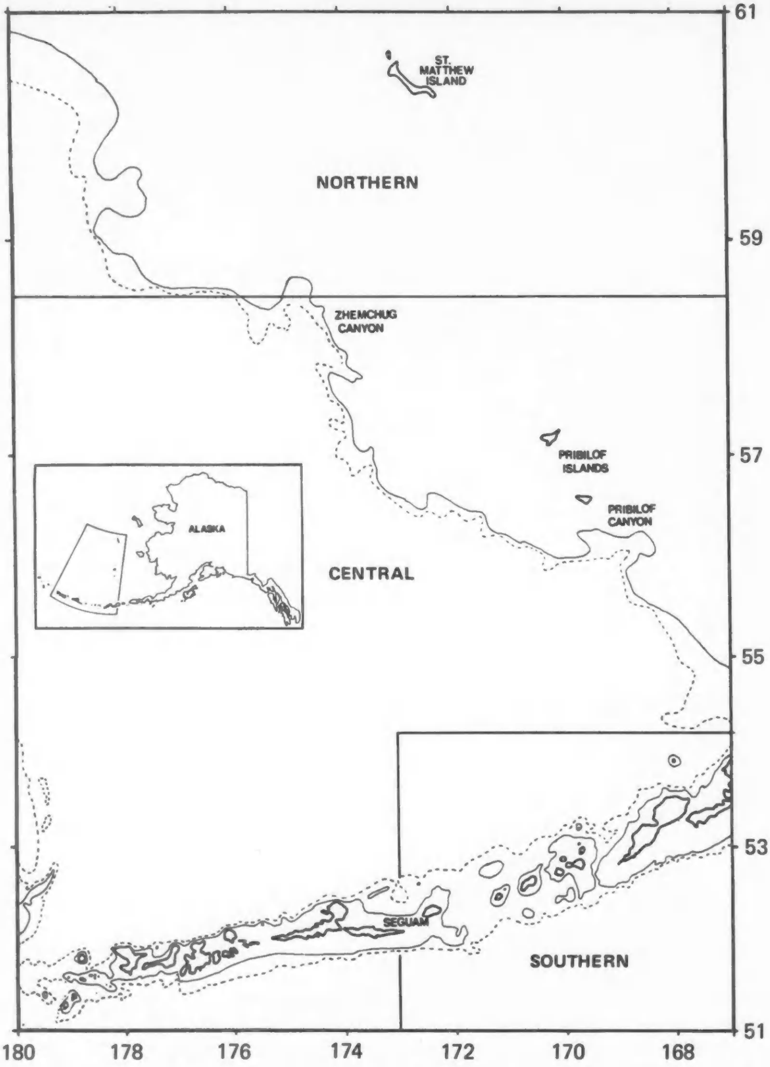
61
59
57
55
53
51
ST. MATTHEW ISLAND
NORTHERN
ZHEMCHUG CANYON
PRIBILOF ISLANDS
PRIBILOF CANYON
ALASKA
CENTRAL
SEGUAM
SOUTHERN
180
178
176
174
172
170
168

FIGURE 1.—Areas of the Bering Sea and eastern Aleutian Islands where golden king crab were sampled by U.S. fishery observers and National Marine Fisheries Service research cruises. Golden king crab occur primarily in a region bounded by the 200 m (solid line) and 1,000 m (dashed line) isobaths. The dark lines indicate the separation of this region into the three latitudinal strata discussed in the text.

Female size at maturity was estimated as the size at which 50% of the crabs were mature. Weighted nonlinear regression (weights equal to the inverse of the binomial variance at each size) was used to fit a logistic equation to the percentage mature within 5 mm size intervals. The fitted logistic equation was then evaluated to determine the carapace length corresponding to 50% maturity. Variance of this size was estimated using the formula provided in Somerton (1980).

BIOLOGICAL VARIATION WITH DEPTH AND LATITUDE

Mean Size

Size-frequency distributions of golden king crab, based on the combined 1981 and 1982 observer data, are shown by sex, area, and depth strata in Figure 2. Linear trends in mean size with depth and latitude were examined statistically using multiple regression. For each sex in each year, when carapace length was regressed against latitude and depth simultaneously, ignoring interaction, both the latitude coefficient and the depth coefficient were negative and highly significant ($P < 0.001$). Averaged over both years, mean size decreased by 6.2 mm for males and by 4.6 mm for females for each 1 degree increase in latitude, and mean size decreased by 7.9 mm for males and by 6.2 mm for females with each 100 m increase in depth.

The latitudinal decrease in size probably reflects a latitudinal decrease in growth rate. Two shallow-water Bering Sea crabs, *Chionoecetes bairdi* and *C. opilio*, also show a latitudinal decrease in size, and this decrease was correlated with a latitudinal decrease in maximum summer water temperature (Somerton 1981a). Although we lack sufficient temperature data from the depths inhabited by golden king crab to allow a statistical test, it is likely that mean annual bottom temperature also decreases

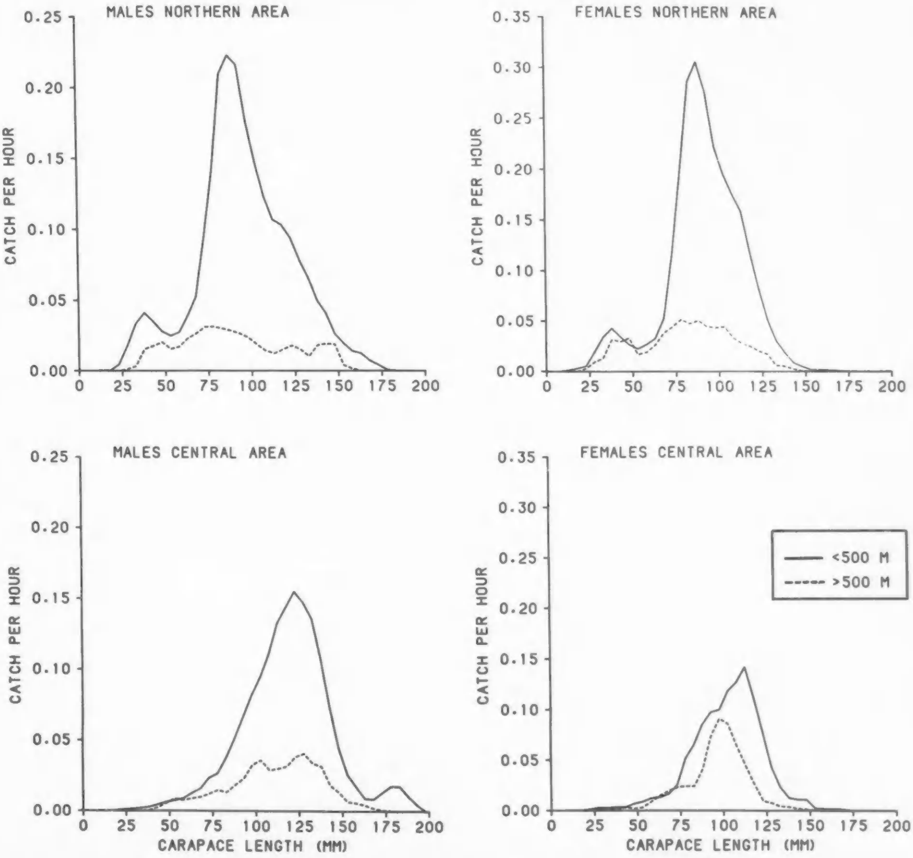

FIGURE 2.—Size-frequency histograms for males and females of golden king crab, by depth strata and subarea. Due to differences in the sampling intensity with depth (Table 2), frequencies have been standardized to catch per hour of trawling.

with increasing latitude along the slope. If this is true, then it is reasonable to assume that growth rates are lower in higher latitudes. Part of the latitudinal decrease in mean size, however, is due to the greater relative abundance of small (25-50 mm) crabs in the northern area (Fig. 2). Since we have only two years of data, we do not know if the greater abundance of small crabs in the northern area is a persistent feature of the distribution. But if it is, it may indicate that greater larval settlement occurs in the northern area because of the advection of larvae by the northwesterly currents over the continental slope (Kinder and Schumacher 1981).

The decrease in size with depth may reflect an ontogenetic upslope migration. Another slope dwelling crab, *Chionoecetes tanneri*, also displays a decrease in size with depth, and this was attributed to an offshore advection of pelagic larvae followed by an onshore migration of juveniles (Pereyra 1968). Although an onshore migration might explain the size variation with depth of golden king crab in the eastern Bering Sea, offshore advection depends on local oceanographic conditions and may not occur everywhere ovigerous golden king crab occur. For example, studies of golden king crab in other areas indicated that adults could be found in shallower water than juveniles (Hiromoto and Sato 1970), or at similar depths as juveniles but in different areas (Rodin 1970) or in deeper water than juveniles (N. Sloan[4]).

Size at Maturity

The change in the relative growth of a male's chela which occurs at maturity is more pronounced for golden king crab than it is for either blue king crab (Somerton and MacIntosh 1983) or red king crab (Somerton 1980), and this allows greater precision in the estimates of size at maturity (Fig. 3). Nevertheless, the estimates of male size at maturity are less precise than those for females (Fig. 4). For both sexes, however, the estimated sizes at maturity differ significantly between areas and progressively decrease with increasing latitude (Fig. 4).

The decrease in the size at maturity is consistent with a latitudinal decrease in growth rate; however, the decrease is greater for males than it is for females (Fig. 4). If golden king crab are similar to red king crab (Weber 1967) in that males and females grow identically while they are immature, then the greater latitudinal decrease in male size at maturity implies that female age at maturity increases, relative to that of males, with latitude. This could occur if females and males have different life history strategies to maximize their reproductive values (Bell 1980). The reproductive value of a female is largely determined by her lifetime fecundity. Since fecundity increases markedly with size and somatic growth decreases abruptly at maturity, under conditions of reduced growth, female reproductive value might be increased by delaying maturity until some optimum size is reached. The reproductive value of a male, however, is largely determined by the number of females he is able to mate with over his lifetime. Unless access to females is strictly limited to the largest males, male reproductive value is unlikely to be increased by delaying maturity. Along a gradient of decreasing growth rate, such strategies would lead to a divergence between male and female sizes and ages at maturity.

Weight at Size

Weight-size relationships of males were determined for each of the three subareas by regressing body weight on carapace length after transforming both variables to natural logarithms. Analysis of covariance showed that the slopes of the regression lines were not significantly different ($F = 0.49$, df $= 2, 1{,}079$, $P = 0.613$), but that the intercepts were significantly different between areas ($F = 19.03$, df $= 2, 1{,}081$, $P < 0.001$). Pairwise *t*-tests further showed that the intercept for each area differed significantly from the other two (Bonferroni critical values; maximum $P < 0.05$) and that the intercepts progressively increased with increasing latitude. Males in higher latitudes are therefore proportionately heavier than equal-sized males from lower latitudes.

This proportionate change in weight with latitude might be due to changes in body shape, such as the relative size of the chelae, that are coincident with the onset of maturity. Since the rate of chela growth increases, relative to carapace growth, at maturity, and since the size at maturity decreases with latitude, mature males in northern areas should have larger chelae than equal-sized males in southern

FIGURE 3.—For the golden king crab males, chela heights, carapace lengths, and the best fitting two line model are shown for each subarea. For the females, percentage mature, within 5 mm size intervals, and the fitted logistic equation are shown for each subarea. Estimated sizes (carapace length) at maturity are indicated by dotted lines.

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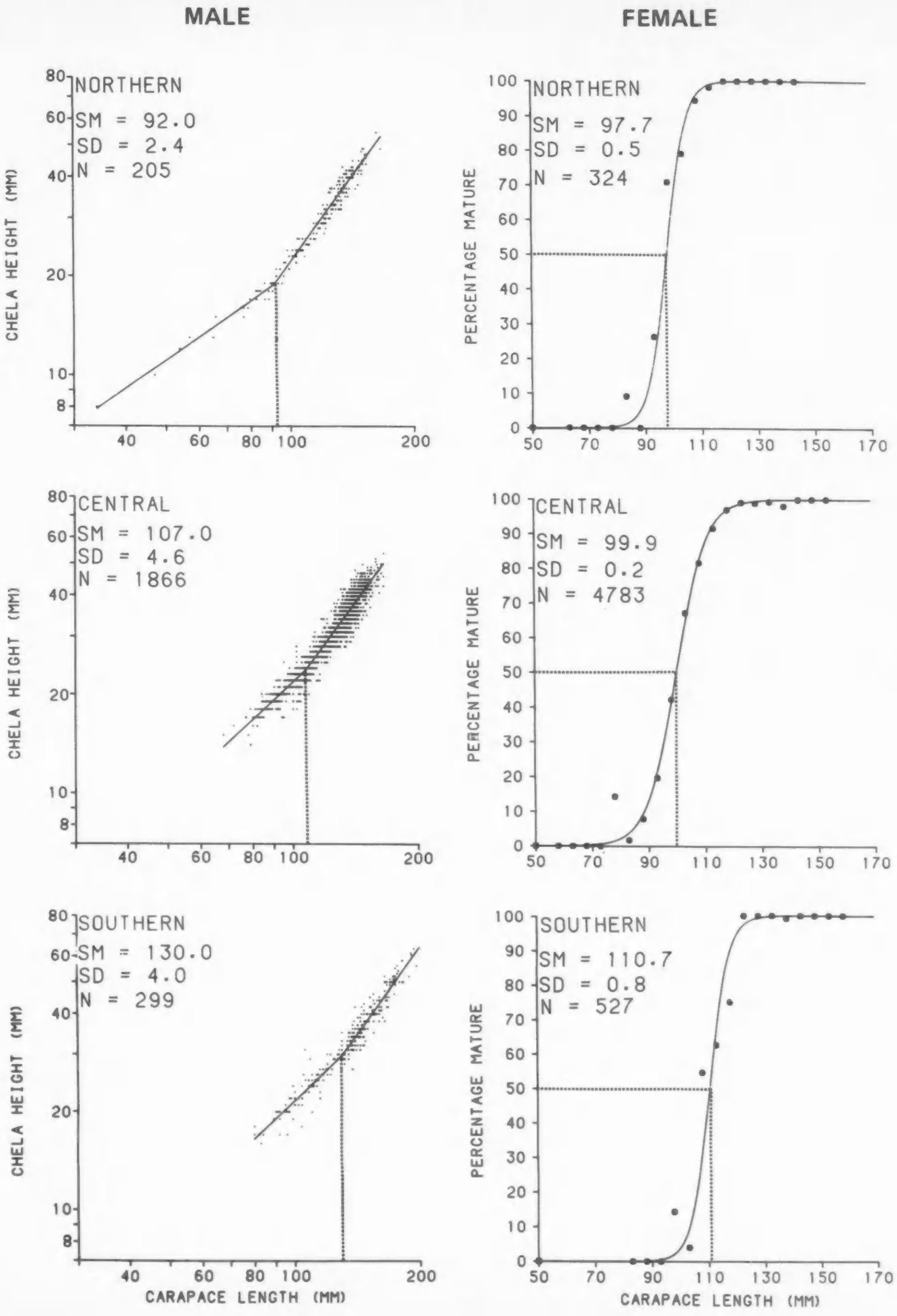
[4] N. Sloan, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada, pers. commun. 1984.


MALE
FEMALE
NORTHERN
SM = 92.0
SD = 2.4
N = 205
NORTHERN
SM = 97.7
SD = 0.5
N = 324
CENTRAL
SM = 107.0
SD = 4.6
N = 1866
CENTRAL
SM = 99.9
SD = 0.2
N = 4783
SOUTHERN
SM = 130.0
SD = 4.0
N = 299
SOUTHERN
SM = 110.7
SD = 0.8
N = 527
CHELA HEIGHT (MM)
PERCENTAGE MATURE
CARAPACE LENGTH (MM)
8
10
20
40
60
80
40
60
80
100
200
0
10
20
30
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50
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90
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70
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110
130
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170

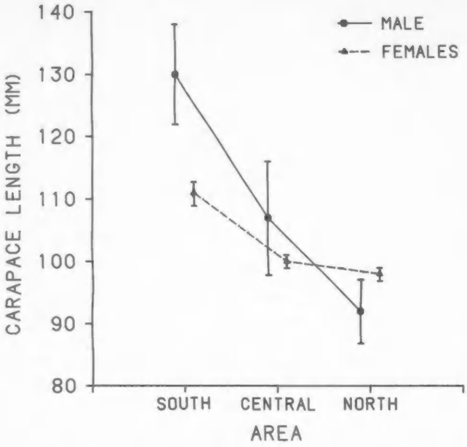

FIGURE 4.—For both sexes of golden king crab, estimated sizes at maturity, and their 95% confidence intervals, are plotted against area.

areas. To test whether this is true, chela height and carapace length relationships for adult males were compared between areas. Analysis of covariance showed that the slopes did not differ ($F = 0.14$, df = 2, 1,998, $P = 0.87$), but the intercepts differed significantly ($F = 146.7$, df = 2, 2,000, $P < 0.001$). Pairwise *t*-tests further showed that each intercept differed significantly (Bonferroni critical values; maximum $P < 0.05$) from the other two and, similar to the weight-size relationships, that the intercepts progressively increased with latitude. Thus northern males, which are the heaviest, have the largest chelae.

By itself, chela size is unlikely to be responsible for latitudinal differences in weight because chela weight is only a small proportion of total body weight. However, chela size may be correlated with other body dimensions (for example, length of walking legs) that also increase relative to carapace length at maturity. We therefore used chela height as a proxy for these dimensions and examined whether the difference in chela height could account for the difference in weight-size relationships. This was done by comparing the weight-size relationships between areas including the logarithm of chela height as a covariate. Two additional modifications of the previous weight-size comparison were made. First, since weights and chela measurements were not obtained from the same crabs in the southern area, the comparison was restricted to the northern and central areas. Second, since chela height and carapace length are linearly related only over the adult (or juvenile) size range, the comparison was restricted to males greater than the size at maturity in each area. When the northern ($N = 129$) and central ($N = 614$) areas were compared considering only carapace length as a covariate, the slopes were not significantly different ($F = 0.06$, df = 2, 739, $P = 0.81$), but the intercepts were significantly different ($F = 7.36$, df = 1, 740, $P = 0.007$). When chela height was included as a covariate, however, neither the slopes ($P = 0.316$) nor the intercepts ($P = 0.430$) differed significantly between areas. This indicates that latitudinal changes in chela size, and perhaps other body measurements that also increase at maturity, account for the observed latitudinal increase in body weight.

Juvenile weight-size relationships were also compared between the northern ($N = 10$) and central ($N = 207$) areas and neither the slopes ($F = 0.06$, df = 1, 213, $P = 0.938$) nor the intercepts ($F = 0.19$, df = 1, 214, $P = 0.664$) were significantly different. The weight-size relationship for male golden king crabs is therefore described by one equation for juveniles and three equations for adults. Transformed back to a linear scale, these relationships are

Juveniles $W = 0.000365\ \mathrm{CL}^{3.099}$ ($N = 217$, $R^2 = 0.88$)
Adults
Northern $W = 0.000225\ \mathrm{CL}^{3.206}$ ($N = 139$, $R^2 = 0.93$)
Central $W = 0.000219\ \mathrm{CL}^{3.206}$ ($N = 632$, $R^2 = 0.91$)
Southern $W = 0.000204\ \mathrm{CL}^{3.206}$ ($N = 100$, $R^2 = 0.91$)

where W is body weight in grams and CL is carapace length in millimeters. Within the adult size range, males from the northern area are 10.3% heavier and males from the central area are 9.8% heavier than equal-sized males from the southern area.

Relative Abundance and Proportion Male

Relative abundance, or catch per hour (CPH), based on combined 1981 and 1982 observer data, is shown by sex, latitude, and depth in Figure 5. Linear trends in CPH with depth and latitude were examined statistically using multiple regression (depth and latitude were considered simultaneously; interaction was ignored). The latitude coefficient for males was not significant ($P > 0.05$) in either year, but the latitude coefficient for females was positive and highly significant ($P < 0.01$) in both years. The depth coefficient for males was negative

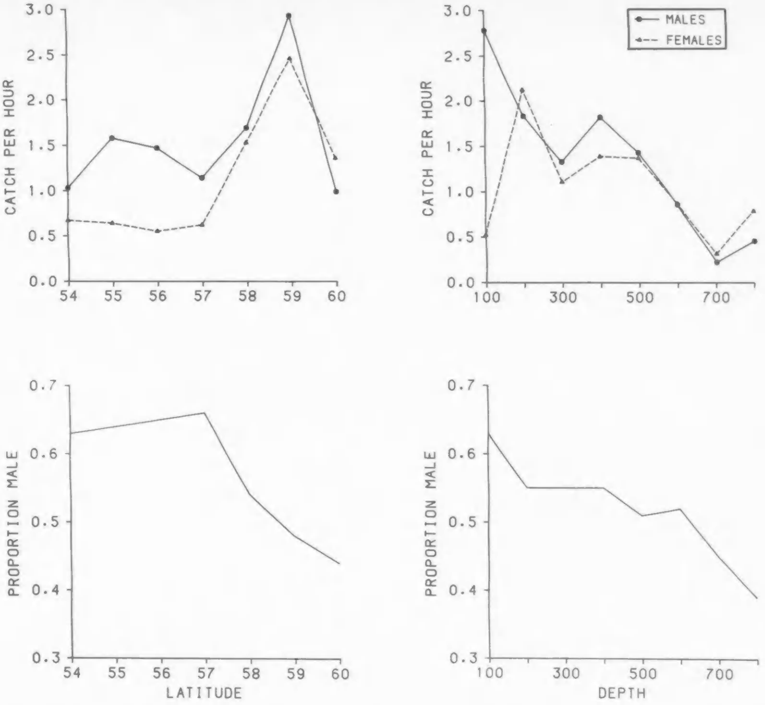

FIGURE 5.—Catch per hour, by sex, and the proportion of males of golden king crab are shown as a function of latitude (left panels) and depth (right panels).

and highly significant in both years ($P < 0.01$), but the depth coefficient for females, although negative in both years, was significant ($P < 0.05$) in only one. Although male CPH decreases significantly with depth whereas female CPH decreases significantly with latitude, CPH is not a strict linear function of depth and latitude; therefore, linear approximations mask aspects of the variability. The important point is that both male and female CPH generally increase with an increase in latitude or a decrease in depth, but at more southerly latitudes or at the shallowest depth, male CPH is considerably higher than female CPH (Fig. 5).

Different trends in CPH between sexes suggested that the sex ratio of golden king crab varied spatially. To investigate this further we examined the variation in proportion of males within trawl hauls having at least five crabs. The proportion of males, based on combined 1981 and 1982 observer data, is shown by latitude and depth in Figure 5. When the proportion of males was regressed against latitude and depth (using weights equal to the number of crabs within each trawl haul), the latitude coefficient was negative and highly significant ($P < 0.01$) in both years; and the depth coefficient, although negative in both years, was significant ($P < 0.05$) in only one.

From a biological perspective, the latitudinal decrease in the proportion of males is difficult to explain; therefore, we considered possible sampling bias that could lead to an apparent change in the proportion of males. Since males are considerably larger than females in the central area but nearly the same size as females in the northern area, the proportion of males might vary with latitude due to size selectivity of the trawls. This hypothesis was tested by comparing the proportion of males between the northern and central areas considering only crabs within an equal size range. To eliminate a possible confounding effect due to a sexual difference in growth rate that begins at maturity, we restricted the comparison to crabs <90 mm. Based on the combined 1981 and 1982 observer data, the proportion of males was 0.51 (N = 1,375) in the central area and 0.43 (N = 8,271) in the northern area. Since the proportion of males still differed significantly between areas (2 × 2 contingency table, $\chi^2 = 30.7$, df = 1, $P < 0.001$), it is unlikely that the change in the proportion of males was due to size selectivity. Furthermore, since the difference in the proportion of males appears to be established before maturity, biological explanations such as sexual differences in migratory behavior or natural mortality are also unlikely.

Although we cannot explain the latitudinal variation in the proportion of males, we believe that the depth variation, especially the abrupt increase in the proportion of males in the shallowest depth zone, is due to sexual segregation. Sexual segregation by depth has been observed for another slope-dwelling crab, *C. tanneri* (Pereyra 1966). Adult female *C. tanneri* occur within a rather narrow depth zone throughout the year while adult males undergo a seasonal migration from relatively shallow water in summer to the deeper water occupied by females during the winter mating period. To determine if golden king crab have a similar seasonal migration, we examined the proportion of males from the northern area at depths <400 m (the northern area had nearly equal sampling in all four seasons). Using pooled 1981 and 1982 data, analysis of variance showed that the proportion of males did not vary significantly between seasons ($F = 0.13$, df = 3, 179, $P > 0.05$). Although adult males of golden king crab probably congregate in somewhat shallower water than adult females, unlike *C. tanneri* this segregation appears to be maintained throughout the year.

REPRODUCTIVE BIOLOGY

Fecundity

Fecundity-size relationships for golden king crab were estimated stagewise by examining 1) the form of the relationship, 2) whether the relationships varied with stage of embryo development, and 3) whether the relationships varied between areas.

The fecundity of king crabs has been reported to increase as either a linear (Haynes 1968) or a curvilinear (Somerton 1981b) function of carapace length. To determine which form was more appropriate for golden king crab, a second degree polynomial was fitted to the fecundity and size data from the northern area (all clutches contained uneyed embryos) and the coefficient of the quadratic term was tested for significance. Since the coefficient was not significantly different from zero ($F = 3.85$, df = 1, 57, $P = 0.06$), we chose a linear relationship to describe the data.

Fecundity-size relationships for females with uneyed embryos (N = 46) and eyed embryos (N = 19) from the central area were compared to determine whether the relationships changed with stage of embryo development. Analysis of covariance showed that the slopes did not differ ($F = 0.77$, df = 1, 61, $P = 0.38$) but that the intercept for eyed embryos was significantly less ($F = 4.89$, df = 1, 62, $P = 0.03$) than that for uneyed embryos. At 114 mm, the median size of adult females in all areas combined, uneyed clutches were 18% greater than eyed clutches. Similar to other crab species (Wear 1974), golden king crab lose a significant number of embryos between egg extrusion and the appearance of embryonic eyes.

Fecundity-size relationships were then compared between the northern (N = 59), central (N = 46), and southern (N = 24) areas considering only those clutches with uneyed eggs. Analysis of covariance showed that the slopes did not differ ($F = 0.74$, df = 2, 123, $P = 0.48$), but the intercepts differed significantly between areas ($F = 4.38$, df = 2, 125, $P = 0.01$). Pairwise t-tests indicated that southern and central intercepts did not differ ($P = 0.99$) from each other, but that both differed significantly ($P = 0.01$, $P = 0.04$) from the northern intercept. Data from the southern and central areas were therefore pooled and compared with those from the northern area. Again, the slopes did not differ ($F = 1.25$, df = 1, 125, $P = 0.27$), but the northern intercept was significantly greater ($F = 8.83$, df = 1, 126, $P = 0.004$) than the pooled central and southern intercept. Assuming equal slopes, the resulting fecundity-size relationships are

$$\begin{array}{ll} \text{Northern} & E = -24815 + 323\ \text{CL} \\ & (N = 59,\ R^2 = 0.79) \\ \text{Central-southern} & E = -26145 + 323\ \text{CL} \\ & (N = 68,\ R^2 = 0.74) \end{array}$$

where E is number of uneyed eggs and CL is carapace length in millimeters. Females from the northern area carry, on average, 1,330 more eggs than equal-sized females from the central and southern areas. For 114 mm females, this represents a 12.6% difference in fecundity.

Northern females may be more fecund than equal-sized central and southern females because they are older and size-specific fecundity often increases with age (Pianka and Parker 1975). But, it is also likely that the observed difference in fecundity is an artifact due to a difference in mean embryo age. We attempted to eliminate the effect of embryo age by considering only clutches with uneyed embryos, but this may not have been a sufficiently sensitive criterion of age and northern females could have had more embryos simply because they had younger embryos. Considering that for equal-sized females the percent difference in clutch size between eyed and uneyed stages was greater than the percent difference in clutch size between areas, it is possible that the loss of embryos within the uneyed stage is sufficient to account for between-area differences. More precise embryo aging techniques are needed to clarify this.

Egg Size

To estimate the size of golden king crab eggs, we considered 1) whether egg size varied with stage of embryo development and 2) whether egg size varied between areas. When mean lengths of uneyed eggs (N = 42) and eyed eggs (N = 26) from the central area were compared, eyed eggs were found to be significantly larger than uneyed eggs (two sample t-test, $P < 0.001$). Golden king crab eggs therefore appear to increase in size, as has been reported for other crab species (Wear 1974), during embryonic development. When mean length of uneyed eggs from the southern (N = 25) and central (N = 42) areas (no egg length data was collected from the northern area) were compared, no significant difference was found (two sample t-test, P = 0.25). Mean length of uneyed eggs, based on the pooled central and southern data, is 2.2 mm (SD = 0.1).

Our estimate of egg length is similar to those reported for Asian populations of golden king crab (2.38 mm, Hiramoto and Sato 1970; 2.30 mm, Suzuki and Sawada 1978), and it is also similar to egg lengths reported for other *Lithodes* species (*L. antarctica*, 2.2 mm, Guzman and Campodonico 1972; *L. couesi*, 2.3 mm, Somerton 1981b). However, this size is more than twice as large as the egg lengths reported for *Paralithodes* species (*P. camtschatica*, 1.0 mm, Haynes 1968; *P. platypus*, 1.2 mm, Sasakawa 1975). The larger eggs of golden king crab are, in turn, reflected in the relatively large size of their first stage zoea (*L. aequispina*, 7.3 mm TL, Haynes 1981; *P. camtschatica*, 4.6 mm TL, Sato and Tanaka 1949; *P. platypus*, 4.9 mm TL, Hoffman 1968). The larger size of *L. aequispina* larvae may allow them to withstand starvation for a longer period or may allow them to capture a wider size range of prey than *Paralithodes* larvae. If this is true, golden king crab larvae may not need to ascend to the photic zone but instead stay at greater depths. Evidence supporting this hypothesis is provided by a study on crab larvae that sampled the upper 50 m near the edge of the eastern Bering sea continental shelf (Fig. 1). Although both *P. platypus* and *P. camtschatica* larvae were found, *L. aequispina* larvae were not (D. Armstrong[5]).

Seasonality of Reproduction

King crabs either can be synchronous and seasonal in their egg extrusion and embryo hatching, as reported for *P. camtschatica* (Powell et al. 1973), or they can be asynchronous and lack seasonal periodicity, as reported for *L. couesi* (Somerton 1981b). To determine which pattern better characterizes golden king crab, we tabulated the percentage of mature females in each of the three reproductive conditions by area and by quarter (Table 3). If the reproductive cycle were synchronous and seasonal, then each of the three categories of reproductive condition should predominate sequentially over the course of a year, but such a pattern is not evident. Regardless of the area or the season in which a sample was collected, all three reproductive categories were always obtained. This suggests that golden king crab have an asynchronous reproductive cycle lacking distinct seasonal variation.

TABLE 3.—Percentage of adult females in each of three categories of reproductive condition: 1) uneyed embryos, 2) eyed embryos, and 3) empty egg cases, and total sample size (N) by subarea and quarter.

	South				Central				North			
Quarter	1	2	3	N	1	2	3	N	1	2	3	N
1	55	33	12	67	50	8	42	12				
2					28	63	9	1,307				
3					14	36	50	1,399	78	3	19	224
4	28	67	5	384	61	16	23	859				

The apparent lack of seasonality conflicts with previous studies of golden king crab reproduction. Hiramoto and Sato (1970) reported that egg extrusion occurs from July to October and embryo hatching occurs from February to July along central Japan. However, Hiramoto and Sato found embryos in late stages of development throughout the year, indicating that embryo hatching was probably occurring at times other than the peak season. Rodin (1970) reported that egg extrusion occurs from August to September based on the relatively high incidence of recently molted females with new embryos. However, Rodin based this on only one summer sample and some of our samples, especially those from the northern area, if examined alone would have also incorrectly led to the same conclusion. Our findings, however, are consistent with those for other deep water crabs (*L. couesi*, Somerton 1981b; *Geryon quinquedens*, Haefner 1978) which have asynchronous or protracted spawning.

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[5] D. Armstrong, College of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. 1984.

Asynchronous spawning is also consistent with two of our other observations. First, the larvae of golden king crab, due to their large size and presumably deep habitat, should be relatively insensitive to seasonal changes in primary production. Second, adult males and females of golden king crab appear to segregate by depth and this segregation appears to be maintained throughout the year. Such year-round sexual segregation is unlikely for a seasonally reproducing species; however, it is consistent with an asynchronous reproducing species if only the reproductively active individuals migrate between depth zones.

IMPLICATIONS FOR FISHERY MANAGEMENT

Two of our findings, the latitudinal decrease in the size at maturity and the asynchronous reproductive cycle, pertain to regulations used to manage the golden king crab fisheries in Alaska.

Commercial harvest of king crabs is restricted to males larger than a minimum legal size (maximum carapace width including spines) which is specified for each species in each management area. These minimum sizes are set at the average size of a male three years after reaching maturity based on the rationale that such a size would preserve sufficient males for breeding even when the exploitation rate is high (North Pacific Fishery Management Council 1981). Thus, to establish a minimum size limit that conforms to this rule, both an estimate of the size at maturity and an estimate of male growth rate are needed. Unfortunately, we lack sufficient data to estimate the growth rates of golden king crab in any of the three management areas considered here and therefore cannot determine appropriate minimum size limits. However, our estimates of male size at maturity can be used to judge, in a qualitative sense, the adequacy of the current minimum size limits. These size limits and the estimated sizes at maturity, expressed in terms of carapace length, are as follows:

	Minimum size limit (mm CL)	*Size at maturity (mm CL)*
Northern area	123	92
Central area	123	107
Southern area	134	130

The current minimum size limits decrease with increasing latitude, but not in proportion to the estimated sizes at maturity. Based solely on the relative magnitude of our estimates, we believe that the current minimum size limit in the southern area, and perhaps in the central area as well, is too low. However, we believe that the prolonged or year-round breeding of golden king crab would allow males more opportunities for mating than would be possible with a short breeding season; therefore, relative to seasonally breeding king crabs, fewer males would be sufficient for the breeding needs of the population. If this is true, then minimum size limits based on the criteria established for red and blue king crabs may be unnecessarily conservative for golden king crab.

Commercial harvest of king crabs is also restricted to a legal fishing season specified for each species in each area. Although economic or logistic factors are considered when fishing seasons are established, of primary importance is the timing of the breeding and molting seasons. During the breeding season, females molt while aggregated together with the males (Powell et al. 1973); and if fishing were permitted at this time, not only would females be caught in greater numbers, they would also be injured by the fishing gear. During and soon after the male molting season, the recovery rate (ratio of recoverable meat to total body weight) is low; and if fishing were permitted at this time, the value of the crabs would also be low. Since the breeding seasons tend to occur in the late winter and early spring and the male molting seasons occur in late spring, the fishing seasons usually begin in the fall. For golden king crab, however, there is no clear seasonality in breeding; and adult males and females appear to be spatially segregated throughout the year. Although we lack sufficient data to determine if there is any seasonality in male molting, it appears that there is no compelling biological reason to restrict the golden king crab fisheries to any particular time of the year. Therefore, we believe that, at present, fishing seasons should be determined primarily by what is most convenient or beneficial to fishermen and processors.

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A MODEL OF THE DRIFT OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE CALIFORNIA CURRENT

James H. Power[1]

ABSTRACT

The drift of northern anchovy, *Engraulis mordax*, larvae in the California Current to unfavorable offshore areas may be an important factor contributing to larval mortality, and hence it may affect recruitment and subsequent adult population size. A simulation model based on a finite-difference approximation to the advection-diffusion equation was developed to aid in the study of larval anchovy drift. Model components included the long-term mean geostrophic and wind-driven current velocities to 50 m depth, and turbulent diffusion. The model predicted larval distributions in the Southern California Bight and offshore regions after 30 days of drift, and these distributions were used to assess the extent of cross-shore and alongshore larval transport that occurs when spawning takes place at different locations, seasons, and during times of increased offshore-directed Ekman transport.

Offshore transport was minimal in most simulations. Simulations of drift starting from the location of peak spawning showed strongest seasonal effects, with currents during the season of peak northern anchovy spawning (March) resulting in reduced offshore dispersal when compared with currents at other times of the year. March currents also produced the greatest downshore (southeasterly) transport of larvae, and strong seasonal currents, such as the nearshore, northwesterly flowing California Countercurrent, can greatly affect the alongshore 30-day larval distributions. Offshore directed Ekman transport, associated with upwelling, does not strongly affect the drift of larvae in the nearshore region, but large increases in overall Ekman transport, or extension of spawning into offshore regions, can result in significant seaward transport of larvae out of the Southern California Bight.

The total population of northern anchovy, *Engraulis mordax*, a common pelagic fish off the west coast of North America, is comprised of three subpopulations (Vrooman et al. 1981): northern (found north of lat. 36°30′N); central (between lat. 29° and 38°N); and southern (south of lat. 29°N). The central subpopulation inhabits the Southern California Bight region, and in recent times has exhibited substantial changes in population biomass (e.g., Smith 1972). Analysis of northern anchovy scales deposited in sediments indicates that large northern anchovy population fluctuations have also occurred in the past few centuries (Soutar and Isaacs 1974). Historically the central subpopulation of northern anchovy has supported a significant fishery (Messersmith and Associates 1969; Sunada 1975; Stauffer and Charter 1982), and although the U.S. fishery has recently declined, there is still a significant Mexican fishery. The northern anchovy fishery, the recent and historical changes in anchovy population size, and the fish's important role in the marine ecosystem all provide the motivation for studying the mechanisms that may cause interannual variations in northern anchovy stock size.

Such changes in stock size may be a consequence of variations in the previous spawning stock size, or they can also arise as a result of interannual differences in mortality during prerecruit life history stages (Rothschild et al. 1982). Because the egg and larval stages have the highest mortalities, it seems possible that processes affecting the relative mortality during these stages can have a significant effect on subsequent recruitment. Two major causes of larval mortality are starvation and predation (Smith and Lasker 1978; Hunter 1981). A factor that may contribute to these is larval drift. The northern anchovy eggs and larvae, lacking adequate motility, can be involuntarily transported away from nearshore spawning areas. It is the nearshore regions in the Southern California Bight that most frequently contain adequate food concentrations for growth and survival of first feeding northern anchovy larvae (Lasker 1978, 1981).

Although eddies and other short-term mesoscale features are important in the Southern California Bight (Mooers and Robinson 1984; Simpson et al. 1984), the broad and relatively slow equatorward flow termed the California Current is the dominant feature in the region that persists on evolutionary

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038; present address: Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State University, Baton Rouge, LA 70803-7503.

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time scales. Hence, it seems plausible that northern anchovy spawning strategies have developed in response to the relatively predictable seasonal and spatial trends in the California Current. Possible relationships between time and location of fish spawning and the currents off the west coast of North America have been discussed by Parrish et al. (1981). They noted that in the Southern California Bight the Ekman (wind-driven) currents are generally diminished relative to other areas along the coast. This reduced offshore transport is favorable for the retention of fish eggs and larvae. However, some weak offshore directed Ekman transport is consistently present in the Southern California Bight year round (Nelson 1977; Parrish et al. 1981; Bakun and Parrish 1982).

Smith (1972) analyzed historical records of northern anchovy larval distribution in the Southern California Bight and found that samples taken farther offshore had a higher proportion of older larvae than that of samples taken nearshore. Assuming a uniform spatial and temporal distribution of spawning, this result implied that a significant fraction of northern anchovy eggs and larvae were transported offshore after nearshore spawning. Bailey (1981) found that the average distance offshore of Pacific hake, *Merluccius productus*, larvae north of Point Conception was positively correlated with offshore Ekman transport and that the magnitude of subsequent Pacific hake recruitment was negatively correlated with offshore transport. Hewitt and Methot (1982) compared the distributions of northern anchovy larvae sampled in 1978 and 1979 and found that the bulk of the larvae in 1979 were farther offshore than those in 1978 and that mortality of 0-group northern anchovy was greater in 1979 when compared with those spawned in 1978. The year 1979 was one of enhanced upwelling and colder temperatures (both concomitants of offshore Ekman transport) relative to 1978.

The studies cited above suggest drift may play an important role in larval ecology, but the conclusions drawn from plankton sampling must be viewed with caution. Inferences drawn from field collections about the drift of larvae usually carry the assumption that both northern anchovy spawning and larval mortality were uniform in space and time, because the time and distance scales involved largely preclude synoptic sampling of eggs and larvae throughout the region. Hence, only correlative explanations for the observed distribution can be made, and other causal factors affecting the larval distribution may be hidden. For example, an observation of greater proportions of older larvae in offshore waters could also result from earlier spawning or greater early mortality (possibly coupled with increased spawning activity) in those waters, and not drift. Additionally, the mesoscale variability present in the Southern California Bight and the considerable patchiness of early and late larvae (due to northern anchovy schooling behavior; Hewitt 1980, 1981a) further confound the conclusions drawn from plankton samples and diminish the value of interannual comparisons. Therefore, as an alternative to field studies, a simulation model of northern anchovy drift in the California Current was developed to help evaluate the role of drift in larval ecology. The objective was to use the model to determine the effect of differences in northern anchovy spawning location and time on the subsequent larval distribution and to evaluate the effects on larval distribution when offshore Ekman transport is increased above its normal mean value.

METHODS

The drift simulation was based on the two-dimensional (x,y) form of the advection-diffusion equation:

$$\frac{\partial F}{\partial t} + \frac{\partial}{\partial x}\left(uF - K_x\frac{\partial F}{\partial x}\right) + \frac{\partial}{\partial y}\left(vF - K_y\frac{\partial F}{\partial y}\right) = 0$$

where F = the concentration of eggs and larvae;
u and v = current velocities in the respective x and y directions; and
K_x and K_y = eddy diffusivity coefficients for the x and y directions.

An analytical solution to this equation cannot be evaluated relative to northern anchovy larval drift in the California Current, although a numerical approximation that specifies larval concentration as a function of location and time can be determined. This was accomplished by approximating each of the derivatives in the equation by weighted finite-differences, so that the model was algebraically formulated as the current and diffusivity-mediated fluxes of larvae among geographic points in the Southern California Bight. Apart from the assumption that larvae continually maintained themselves in surface waters, the northern anchovy were assumed to be conservative and completely passive drifters, i.e., no mortality or movement due to larval swimming was incorporated into the model. Details of the numerical methods used are presented in Power (1984).

The geographic grid for the model was defined using the California Cooperative Oceanic Fisheries Investigation (CalCOFI) coordinate system. The CalCOFI grid is a regular coordinate system of cross-shore "lines" and alongshore "stations". The model and CalCOFI grids are oriented with respect to the coast so that increasing station number corresponds to increasing offshore distance and increasing line number implies the downshore (southeasterly) direction. Each line unit increment is spaced 12 nm apart, and each station unit represents 4 nm. The grid for the model was defined to form cells that were 37 km (20 nm) on a side, and the fluxes of larvae were among grid cell centers. Model coverage was from CalCOFI lines 70 to 120, and extended offshore to CalCOFI station 120 (Fig. 1).

Unless northern anchovy utilize a strategy whereby spawning is initiated in response to the presence of an eddy or other short-term mesoscale features, it can reasonably be expected that spawning time and location have evolved partially in response to predictable current features. For this reason, seasonal currents based on interannual means were used in the model. Northern anchovy spawning behavior relative to eddies, etc., is presently unknown, and there are persistent seasonal trends in spawning, e.g., northern anchovy spawn throughout the year, but March is typically the peak time of spawning (Smith 1972; Methot 1981).

Geostrophic currents for the model were calculated using the geopotential anomalies computed by Lynn et al. (1982). Lynn et al. used CalCOFI data collected between 1950 and 1978 to compute the average geopotential anomaly relative to 500 m for four seasonal periods (nominally January, April, July, and October) at 175 locations in the California Current. Average geopotential anomalies were computed for an additional 23 locations for this study to augment the Lynn et al. (1982) coverage

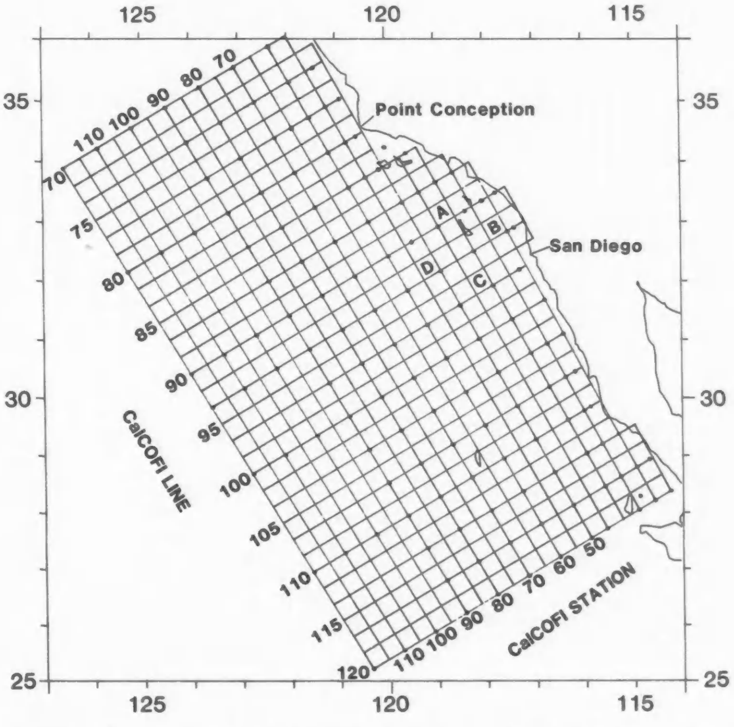


FIGURE 1.—Geographic grid used in the northern anchovy drift simulations, and the corresponding CalCOFI line and station coordinate system. Lettered locations are starting points for simulation presented in this paper. Mean geopotential anomolies (used for computing geostrophic currents) were calculated for the locations indicated by dots (Lynn et al. 1982; this study).

(Fig. 1). The top 50 m of the water column is the predominant depth range of anchovy larvae (Ahlstrom 1959), therefore mean anomaly values for the surface and for 10, 20, 30, and 50 m of depth were used in this study. The anomalies at each standard depth were interpolated to model grid nodes using the bivariate interpolation algorithm of Akima (1978). Geostrophic current velocities normal to each grid cell interface were computed for each of the standard depths, and average geostrophic current velocities were then calculated for a layer extending from the surface to 50 m.

Wind speed and direction data used in this study were from the data base summarized and discussed by Nelson (1977). The raw wind observations were converted to surface wind stress (τ) values using the relation

$$\tau = \rho C_d W^2$$

where ρ = air density (1.22 kg m^{-3});
C_d = drag coefficient; and
W = wind speed.

The drag coefficient was computed as a function of wind speed using the empirical relation of Amorocho and DeVries (1980, 1981). The computed wind stress vectors were partitioned by month of observation and resolved into alongshore and cross-shore components. A monthly mean wind stress component for each model grid cell interface was then computed by averaging the appropriate component of the stress vectors in the 37 km by 37 km area bisected by the grid cell interface. Total Ekman or wind-driven transport in the direction 90° to the right of the wind can be approximated by dividing the wind stress by the Coriolis parameter (Neumann and Pierson 1965), and this calculation was performed for the mean wind stress components. The mixed layer depth in the California Current is seldom >50 m, and is often <20 m in the Southern California Bight during the summer (Husby and Nelson 1982). It was assumed that Ekman transport occurring deeper than 50 m was negligible, and the Ekman transport values were converted to a mean wind-driven velocity for the surface to 50 m layer by dividing the transport by the 50 m layer thickness.

The final current velocities were calculated as the vector sum of the seasonal geostrophic and appropriate monthly Ekman components. Vector addition of the two components appears to be a reasonable assumption (Parrish et al. 1981), and no compensation for redistribution of mass owing to sustained winds was performed. The final seasonal current fields for the simulations were January, March (April geostrophic velocities plus March Ekman velocities), July, and October currents.

Figure 2 illustrates the general trends in the California Current for the January and March seasons. This figure should be interpreted with caution. Apart from the large potential differences between actual synoptic conditions and the average pattern used in the simulations, the resultant vector for a cell was necessarily computed for Figure 2 by averaging the current components of opposing cell faces and then calculating the resultant. A distortion is introduced wherever components on opposite faces of a cell differ in magnitude or sign, so that Figure 2 best represents features of the California Current that are consistent over several model grid cells. The California Current is evident as two regions of intensified southeasterly flow at the left margins and midlines of the plots. During all parts of the year except spring, the current turns toward shore at the southern end of the Southern California Bight. A northwesterly flow near the coast subsequently forms the inshore portion of a large cyclonic eddy (the Southern California Eddy; Owen 1980) that occupies most of the Southern California Bight. During most of the year part of this eddy's northeasterly flow continues past Point Conception, to form the California Countercurrent (Hickey 1979; Fig. 2, January plot). In the spring the southeasterly flow of the California Current moves closer to shore to obliterate the surface portion of the Countercurrent (Fig. 2, March). Tsuchiya (1980, fig. 2) gives a clear picture of the seasonal inshore-offshore movements of the California Current at CalCOFI lines 90 and 93. Close to shore in the southern half of the modeled region there is another region of intensified southeasterly flow, most evident in the March current plot. Lynn et al. (1981) provided detailed illustrations of the geostrophic flow regimes used in the simulations, and Nelson (1977) presented graphical representations of the wind stress fields along the west coast of North America. Hickey (1979) presented a comprehensive review of seasonal and spatial variations of the California Current and the possible driving mechanisms involved, and Owen (1980) reviewed the incidence and ecological consequences of eddies in the California Current system.

Two additional current fields were calculated in order to assess the effects of increased offshore directed Ekman transport on larval northern anchovy distribution. As mentioned earlier, the mean wind stress is consistently directed downshore during March in the modeled region, a condition

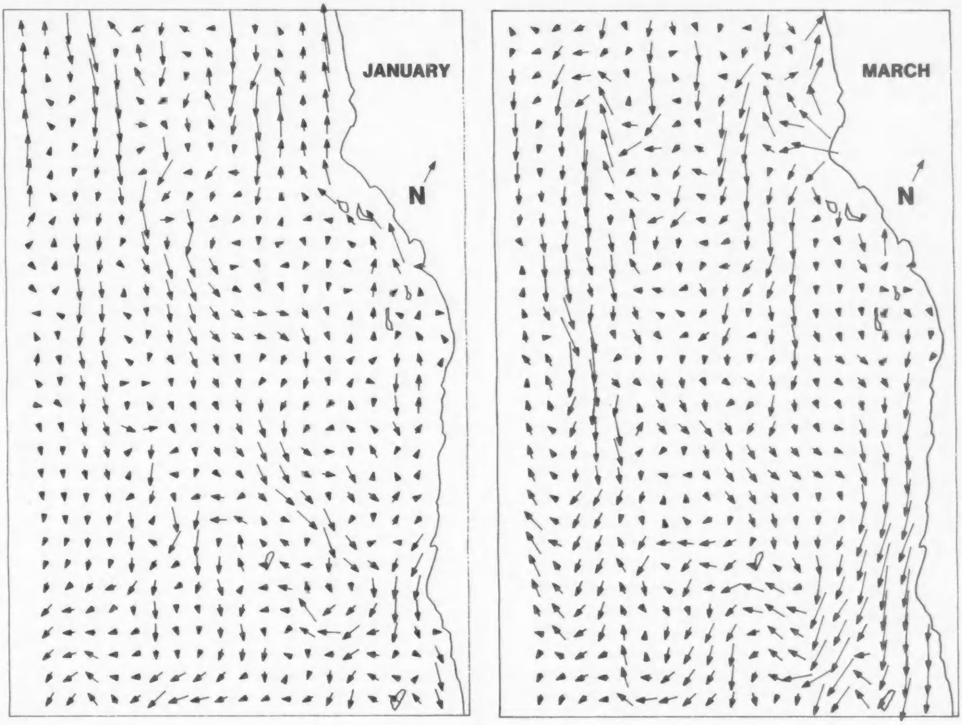


FIGURE 2.—Resultant mean current vectors for the normal January and the March seasonal current data used in this study. See text for cautions concerning figure interpretation. Length of arrow indicating north direction corresponds to a current velocity of 10 cm/s.

producing offshore directed Ekman transport. Two current fields were obtained by increasing the cross-shore component of the mean March Ekman velocities by the factors 1.5 and 3.0, and then combining the April seasonal geostrophic and augmented March Ekman velocities. Wind stress, and hence transport, is proportional to the square of wind speed. This means that roughly a 22% increase in a downshore wind speed increases the corresponding offshore directed Ekman transport by the factor 1.5. A threefold increase in offshore Ekman transport results from about a 77% increase in the downshore wind speed. Bakun and Nelson (1976) presented extensive statistical analyses of an "upwelling index" (defined as the offshore directed component of Ekman transport) for the location lat. 33°N, long. 119°W (this point is very close to location A used in the simulations; see below). Over an annual cycle the mean upwelling index for this location changes by at least a factor of two, with a rapid increase in both mean and standard deviation during the spring. The March mean index at this point was about 50 t/s per 100 m of coastline with a standard deviation of roughly 80, hence upwelling at this particular time and location can be highly variable. Further, Bakun and Nelson (1976) found that enhanced or diminished upwelling persists on a seasonal time scale, so incorporation in the model of prolonged increased Ekman transport was not unrealistic.

Diffusion was incorporated into the model solely to parameterize subgrid scale mixing; including larger scale and more ephemeral mixing processes would obscure the broad seasonal trends the model was intended to illustrate. The eddy diffusivity parameter was computed using scale-dependent diffusion formulae of Okubo (1976) and a regression analysis of diffusion data presented by Okubo (1971). The finite-difference representation of diffusion required the use of a pseudo-Fickian diffusivity coefficient, so the mean scale-dependent diffusivity for the 37 km grid spacing ($K_x = K_y = 101$ m^2/s) was used for all locations and all times in the model. The numerical method incorporated diffusion as the weighting factor $\coth[(uh)/(2K)]$ for the flux at each grid cell interface, where u is the current velocity at the interface and h is the 37 m grid spacing (see Power 1984 for further details). Hence, diffusion becomes important in regions of low current velocity, and at higher velocities diffusion is less important and advection dominates the flux. For the current velocities in most of the modeled region, the above hyperbolic cotangent function is usually evaluated to a magnitude near unity, making the contribution of turbulent transport to larval drift minimal relative to advective (current velocity) transport.

Simulations were carried out by starting an initial point source of northern anchovy eggs or larvae at various locations historically known to be larval anchovy habitat (Hewitt 1980). Examples of simulations for four starting locations (Table 1; Fig. 1), which are representative of the overall patterns produced by the simulations, are presented here. The four locations will be referred to in the text by their letter designations indicated in Figure 1 and Table 1. Northern anchovy larvae begin to school at about 27 d (Hunter and Coyne 1982); therefore larval distributions after 30 d of drift are presented. Thirty-d-old larvae are also rapidly increasing their "patchiness" (Hewitt 1981a), indicating that they could then exert significant control over their position. The time step in the simulations was 1 d. Results from a simulation using the actual northern anchovy egg distribution found in 1982 as the initial condition can be found in MacCall (1983).

TABLE 1.—Geographic and CalCOFI coordinates of starting locations for simulations presented in this paper. Letter designation corresponds to the same locations in Figure 1.

Starting location	Coordinates		CalCOFI	
	Lat. N	Long. W	Line	Station
A	33°08.4′	118°51.4′	89.17	42.5
B	32°54.1′	117°47.3′	92.5	32.5
C	31°59.3′	118°05.4′	95.83	42.5
D	32°14.1′	119°09.2′	92.5	52.5

Northern anchovy larval concentrations in the contour plots are relative to starting concentration; the unitless contour value of 10^{-2} represents a larval concentration two orders of magnitude below the starting concentration, and only concentrations down to 10^{-7} are illustrated. Larvae were permitted to be advected out the borders of the modeled area, except for the border along the coast. Grid cells bordering the Santa Barbara Channel (at about lat. 34°N, long. 120°W; Fig. 1) between the Channel Islands and Point Conception were open, and larvae advected into this region were considered to be lost from the system. Larvae were not permitted to be transported across any of the islands in the modeled region. Because March is the peak spawning time of northern anchovy, the effects of different starting locations on the 30-d larval distributions during March conditions will be presented first. The effects of spawning in different seasons and enhanced offshore Ekman transport during March will then be presented for comparison. The simulation results nominally represent larval northern anchovy distributions, but the results also apply to any planktonic species that begin drift at the same locations and maintain themselves in the top 50 m of the California Current.

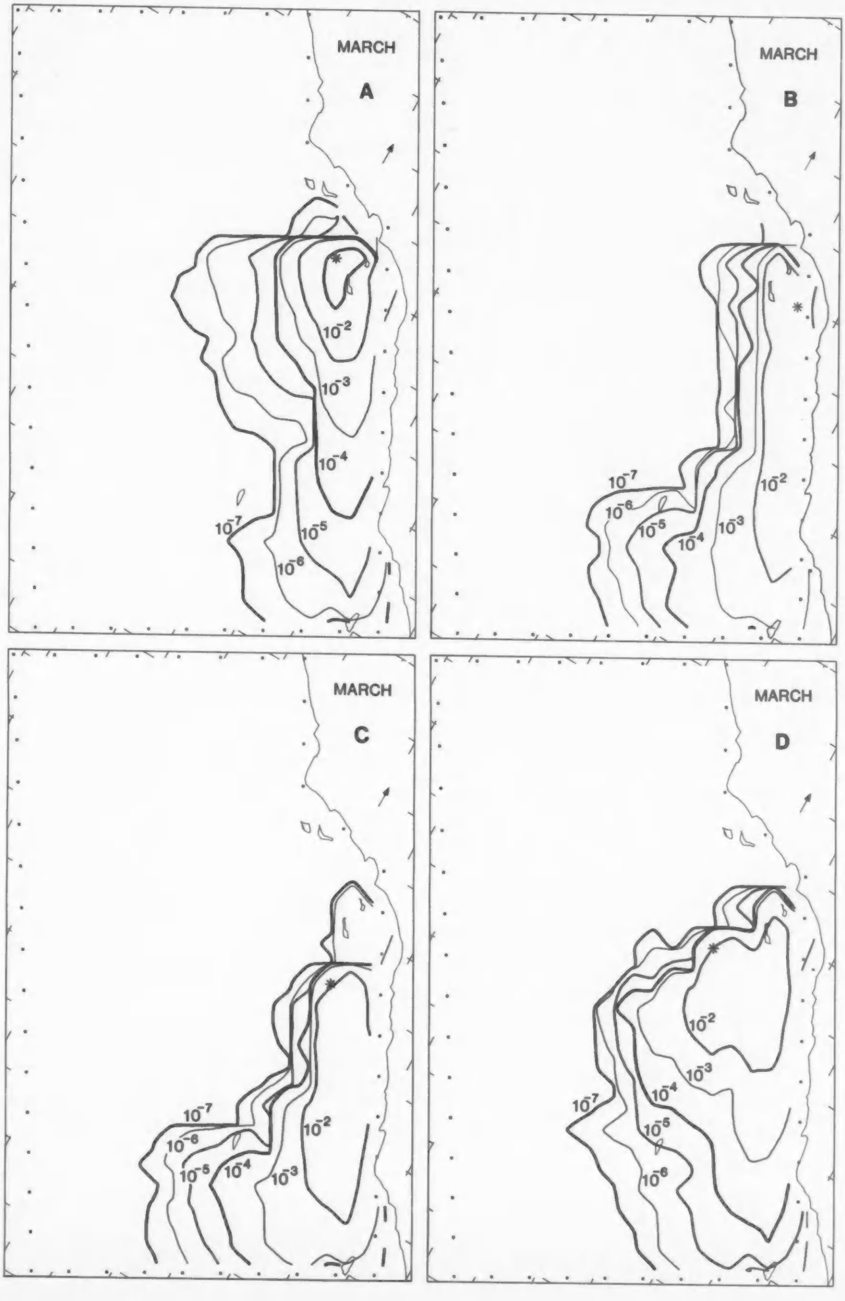
The overall extent of onshore-offshore and alongshore transport was of major interest in this study. A convenient way of summarizing the simulated larval distributions relative to their cross-shore distribution was to sum all larval concentrations in the cells having the same CalCOFI station coordinates. These sums were converted to percentages of the total number of larvae at 30 d, and the cumulative percentage of larvae present as one progressed offshore was plotted versus CalCOFI station coordinates. A similar procedures using CalCOFI line coordinates was done to summarize alongshore transport.

RESULTS

Effects of Starting Location, Normal March Currents

Northern anchovy larvae that began drift at location B, near the coast, were transported downshore by March currents (Fig. 3B). This was an effect of the nearshore southeasterly current (Fig. 2), and because of this flow only 15% of the larvae were at or upshore of the starting location after 30 d of drift

FIGURE 3.—Distribution of northern anchovy larvae after 30 d of drift in March currents. Letter designation corresponds to a simulation with northern anchovy begun at the corresponding lettered location in Figure 1 and Table 1; starting location is marked in this and subsequent contour plots with asterisks. Locations A and C share the same CalCOFI station coordinate; points B and D have the same CalCOFI line coordinate. Concentration contour intervals are proportions of the starting concentration, decreasing in order of magnitude steps. Tic marks around perimeter are at whole degrees of latitude and longitude; dots are at intervals of 3.33 CalCOFI line units from lines 70 to 120 and intervals of 10 station units offshore to station 120 (i.e., every 74 km).


MARCH
A
10⁻²
10⁻³
10⁻⁴
10⁻⁵
10⁻⁶
10⁻⁷
MARCH
B
10⁻⁷
10⁻⁶
10⁻⁵
10⁻⁴
10⁻³
10⁻²
MARCH
C
10⁻⁷
10⁻⁶
10⁻⁵
10⁻⁴
10⁻³
10⁻²
MARCH
D
10⁻²
10⁻³
10⁻⁴
10⁻⁵
10⁻⁶
10⁻⁷

(Fig. 4). The alongshore distribution of larvae below the starting point was quite uniform, and the lower larval concentrations had reached the southern border of the modeled region (CalCOFI line 120). Dispersal offshore was minimal, and a majority of the larvae lay in a band near the coast with about equal proportions inshore and offshore of the starting point; 92% of the larvae were on or inshore of CalCOFI station 37.5. After initial southeasterly transport, some larvae were transported in an offshore, southwesterly direction.

Extensive downshore transport also occurred to northern anchovy larvae begun at location C, and in fact only 3% of the larvae remained at or upshore of the starting location after 30 d of drift (Figs. 3C, 4). The larvae begun at point C were also concentrated in a narrow band along the coast, but unlike those started at point B most of the larvae begun at C moved inshore of the starting location after 30 d of drift.

Northern anchovy larvae begun at the offshore location D showed much less extensive downshore transport than those begun at B or C (Figs. 3D, 4). Only 10% of the larvae remained at or upshore of the starting point, but 86% of the total remained at or between CalCOFI line 92.5 (location C's line coordinate) and line 102.5, a span of 222 km. Most larvae were inshore of location D, and the cross-shore distribution was slightly more uniform than those begun farther inshore. Starting point D's distance from the coastline permitted the slightly broader cross-shore distribution.

Larvae begun at location A showed an alongshore cumulative percentage distribution after 30 d of drift which was similar to that of larvae that begin drift at point D, although it was displaced farther upshore (Fig. 4). Location A produced the greatest percentage of larvae remaining at or upshore of the starting location, and there is a small patch of high (10^{-1}) larval concentrations present at the starting location (Fig. 3A). This reduced dispersal of larvae begun at A also produced the strongest cross-shore gradient of larvae. A majority of the larvae were again on or inshore of the starting location after 30 d of drift.

In summary, the distributions of northern anchovy larvae that began drift at locations A through D and that were produced by March currents were formed as relatively strong cross-shore gradients, so that the 30-d distributions were bands (ca. 100 km wide) parallel to the coast. The results of starting larvae at locations A, C, and D were that more than 85% of the larvae were inshore of the starting location after 30 d of drift. Larvae that began drift at locations B and C were extensively carried downshore of the starting location. Most of the larvae that started at points A and D also moved downshore from those locations, but the bulk of the larvae were not as widely dispersed from the starting location as those begun at points B and C.

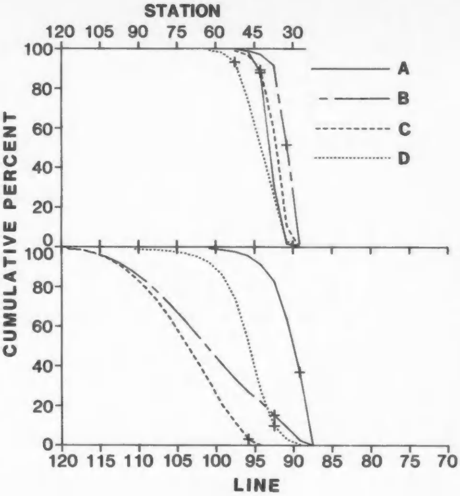


FIGURE 4.—Cumulative percentages of northern anchovy larvae after 30 d of drift, progressing offshore (increasing CalCOFI station number) and downshore (increasing CalCOFI line number), for the four starting locations under March current conditions. Cross symbols are at the starting location's corresponding CalCOFI line or station coordinate. Distance between tic marks on the abscissae is equivalent to a distance of 111 km. Note that a steep curve implies a compact distribution of larvae, while more gradual slopes imply more widely dispersed larvae.

Effects of Seasonal Current Fields on Larval Distribution

The distributions of northern anchovy larvae started at the same location but using different seasonal current regimes appear very different to the eye (Figs. 3, 5-7). Part of this effect is real, but part is also due to displacement of the contours for the lower larval concentrations (e.g., 10^{-7}), which represent few larvae. The cumulative percentage plots (Fig. 8) indicate that, when summarized on a model-wide basis, the overall cross-shore distributions of larvae begun at locations B, C, and D were not greatly different when currents from the four seasonal periods were used in the simulations. A fixed distance offshore there were some large differences in the cumulative percentages among seasons

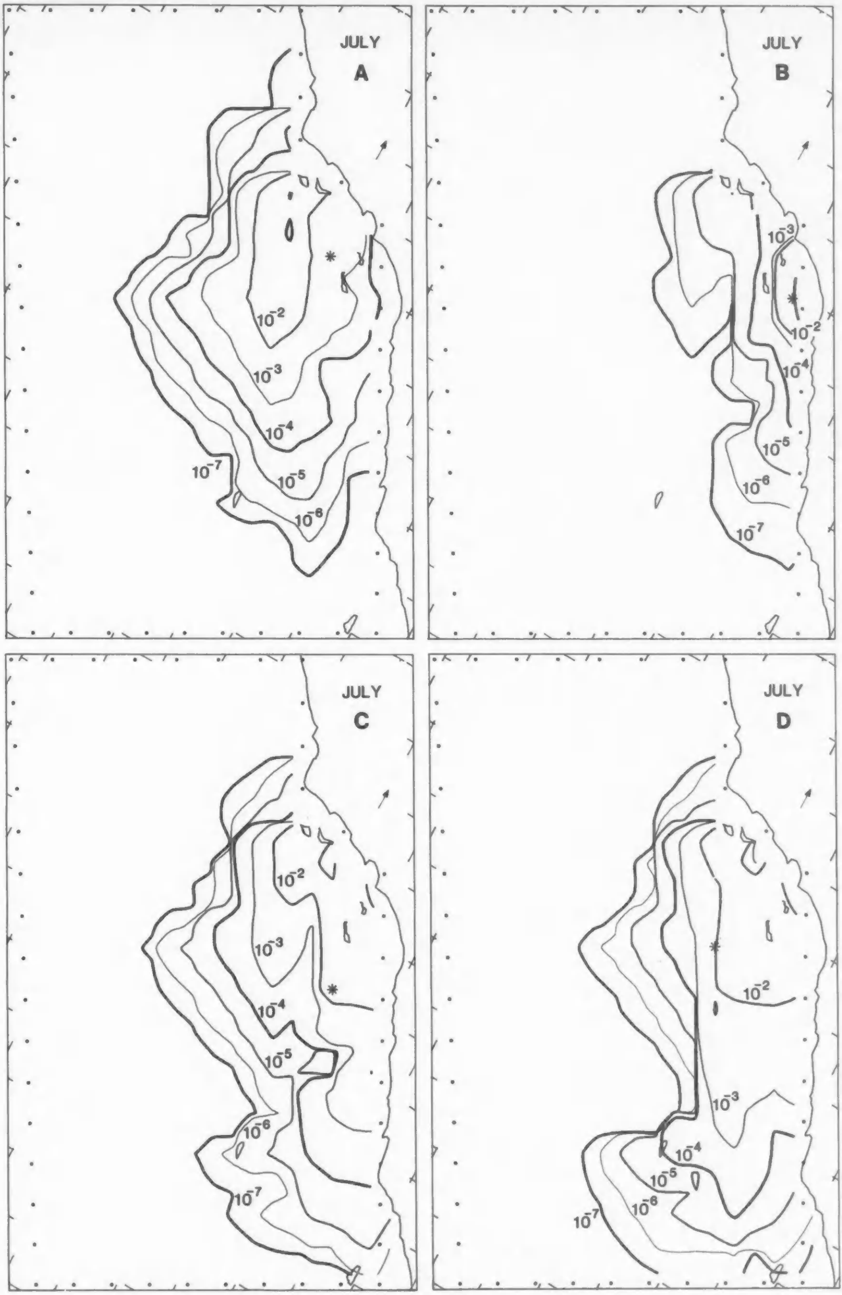

JULY
A
10^{-2}
10^{-3}
10^{-4}
10^{-7}
10^{-5}
10^{-6}
JULY
B
10^{-3}
10^{-2}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
JULY
C
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
JULY
D
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}

FIGURE 5.—Distribution of northern anchovy larvae after 30 d of drift in normal July currents.

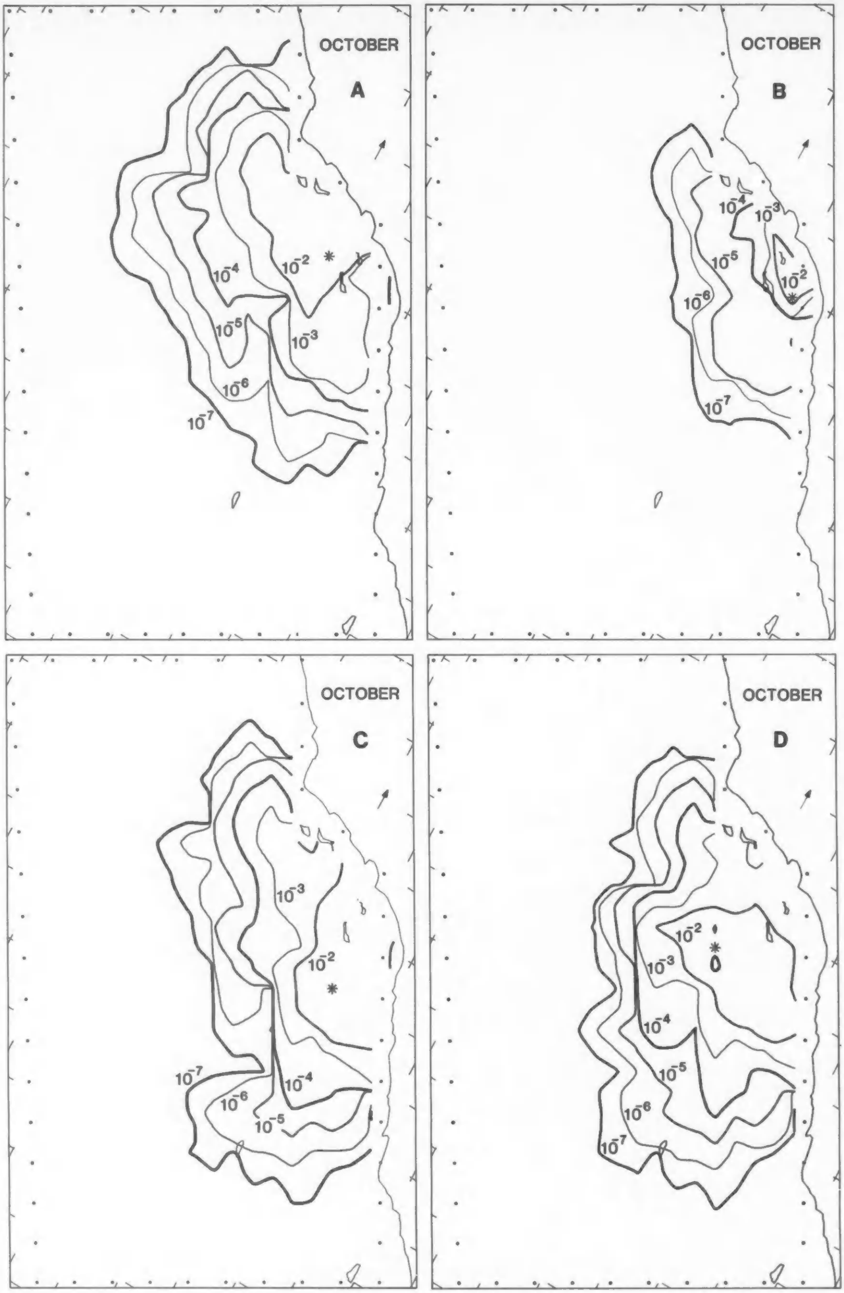

OCTOBER
A
10^{-4}
10^{-2}
10^{-5}
10^{-3}
10^{-6}
10^{-7}
OCTOBER
B
10^{-4}
10^{-3}
10^{-5}
10^{-2}
10^{-6}
10^{-7}
OCTOBER
C
10^{-3}
10^{-2}
10^{-7}
10^{-4}
10^{-6}
10^{-5}
OCTOBER
D
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}

FIGURE 6.—Distribution of northern anchovy larvae after 30 d of drift in normal October currents.

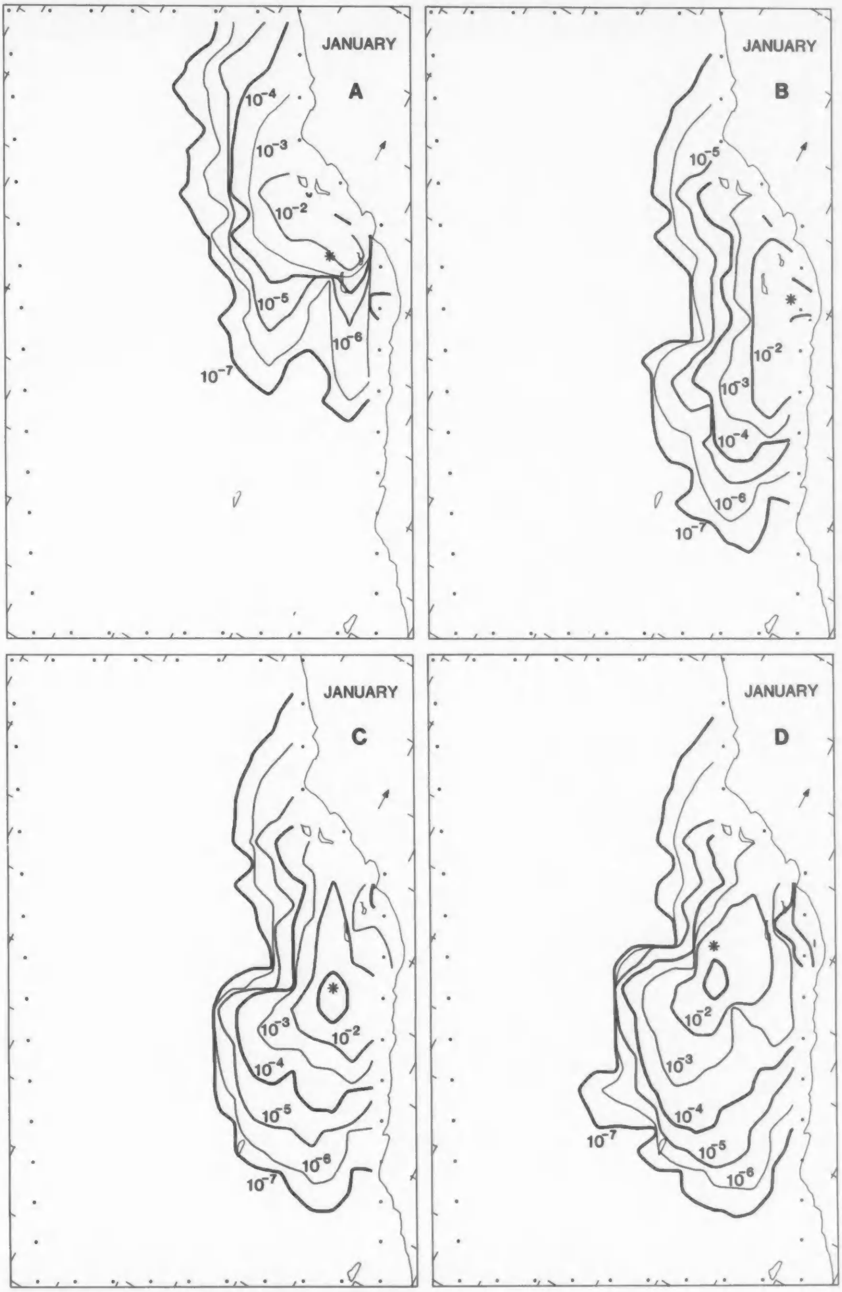

JANUARY
A
10^{-4}
10^{-3}
10^{-2}
10^{-5}
10^{-6}
10^{-7}
JANUARY
B
10^{-5}
10^{-2}
10^{-3}
10^{-4}
10^{-6}
10^{-7}
JANUARY
C
10^{-3}
10^{-2}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
JANUARY
D
10^{-2}
10^{-3}
10^{-4}
10^{-7}
10^{-5}
10^{-6}

FIGURE 7.—Distribution of northern anchovy larvae after 30 d of drift in normal January currents.

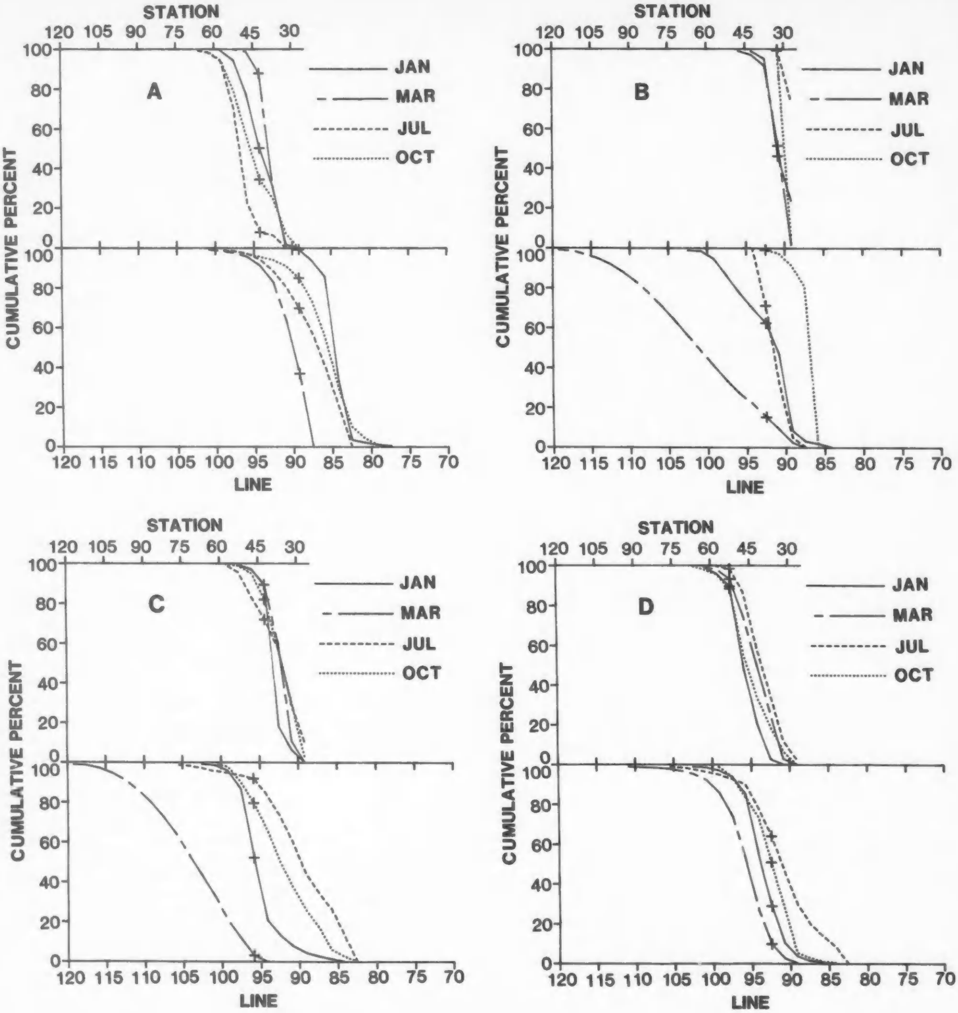


FIGURE 8.—Cumulative percentage plots of northern anchovy larval concentrations after drift in the four seasonal current regimes. Letter designation corresponds to starting locations indicated in Figure 1 and Table 1.

for larvae begun at the same location, but a comparable percentage was usually present a short distance away, i.e., most curves in Figure 8 are closely spaced on the CalCOFI station abscissae. Most larvae begun at the offshore location D moved inshore regardless of season, and the seasonal differences were in the relative extent of inshore movement, the maximum occurring during July. In all simulations the cross-shore distributions of larvae formed strong gradients, regardless of season.

Starting location A is within the Southern California Bight proper, the region that most consistently has high larval concentrations of northern anchovy (cf. Hewitt 1980). Larval distributions started at location A did exhibit notable seasonal differences in their 30-d cross-shore distributions, with the greatest offshore dispersal occurring during July (Figs. 5A, 8A), and the largest inshore movement occurring during March current conditions (Figs. 3A, 8A). January and October were intermediate between these two extremes. In all cases the cross-shore gradients of larvae were strong.

In contrast, the alongshore distributions of larvae differed markedly when the simulations were done with currents from the four seasonal periods. Virtually all larvae were carried upshore of starting location A by the California Countercurrent in the January simulation (Figs. 7A, 8A), but when the model was run using March currents, a majority of the larvae were downshore of point A after 30 d of drift (Fig. 3A). The July and October simulation results for point A seemed to indicate an annual progression between the March and January extremes (Fig. 8A).

The seasonal differences in the overall alongshore distributions were even more dramatic for northern anchovy larvae begun at locations B and C. The uniform downshore distribution produced by March currents differed from the distributions formed in all other seasons. Larvae begun at location B were all transported upshore of the starting location during October current conditions (Fig. 6B). When January currents were used (Fig. 7B), the upshore movement had lessened, so that only 62% of the larvae were at or upshore of location B, and the larvae were more evenly distributed along the coast (Fig. 8B). March currents yielded the greatest downshore movement, and the July distribution (Fig. 5B) was intermediate between that produced by March and October conditions, with the alongshore gradient of larvae again steepening. The changes on an annual basis between upshore, then downshore transport were similar for larvae begun at location C, except that the July current conditions produced the greatest upshore transport (Figs. 5C, 8C); March again produced the maximum downshore transport for larvae begun at point C (Fig. 3C). Larvae begun at location C formed a relatively compact distribution after 30 d of drift in the January currents (Fig. 7C).

The overall alongshore distributions of northern anchovy larvae that started drift at point D appeared to be least influenced by seasonal changes in the currents, although March conditions again produced the greatest transport downshore of the starting point (Fig. 3D), with July currents again yielding the greatest upshore transport (Fig. 5D). January currents also produced a very compact distribution of larvae started at location D, similar to that of larvae begun at point C.

In summary, only northern anchovy larvae begun at location A appeared to have notable differences in their model-wide, cross-shore distributions after 30 d of drift. Larvae begun at all four locations did have substantial seasonal differences in their alongshore distributions, with March currents consistently producing the greatest downshore dispersal. The least downshore dispersal occurred during January, October, July, and July current conditions for larvae started at locations A, B, C, and D respectively. January currents generally seemed to produce the most compact 30-d distributions of larvae (least dispersal).

Effects of Increased Offshore Ekman Transport, March Currents

Increasing the March cross-shore Ekman transport by a factor of 1.5 had little effect on the 30-d distributions of northern anchovy larvae begun at locations B and C (Fig. 9); these curves are also closely spaced on the CalCOFI station abscissae. Increasing the average or "normal" offshore Ekman component by a factor of three produced more noticeable changes in the cross-shore distributions of larvae begun at points B and C, but this effect was not substantial; the contours representing the lower concentrations extended far offshore (Fig. 10B, C), but the higher concentration contours, which delimit the majority of the larvae, were not greatly displaced from those of normal March currents (Fig. 3B, C). This is also evident in the cumulative percentage curves.

In comparison, northern anchovy larvae begun at locations A and D underwent about the same increase in offshore dispersal with a 1.5× offshore directed Ekman component increase as those begun at points B and C did with the 3× offshore Ekman increase (Fig. 9). When the offshore directed Ekman transport was increased to three times its normal mean value, the effects on larvae begun at points A and D were substantial. A majority of the larvae were carried offshore of starting locations A and D, and a large fraction were transported a significant distance (Fig. 10A, D), well seaward of the Southern California Bight. The increase in offshore Ekman transport also noticeably affected the alongshore distributions of larvae begun at locations A and D (Fig. 9). The overall pattern of alongshore distribution is similar to that produced by the normal mean conditions, but the larvae were generally farther downshore.

DISCUSSION

Models have inherent assumptions and simplifica-

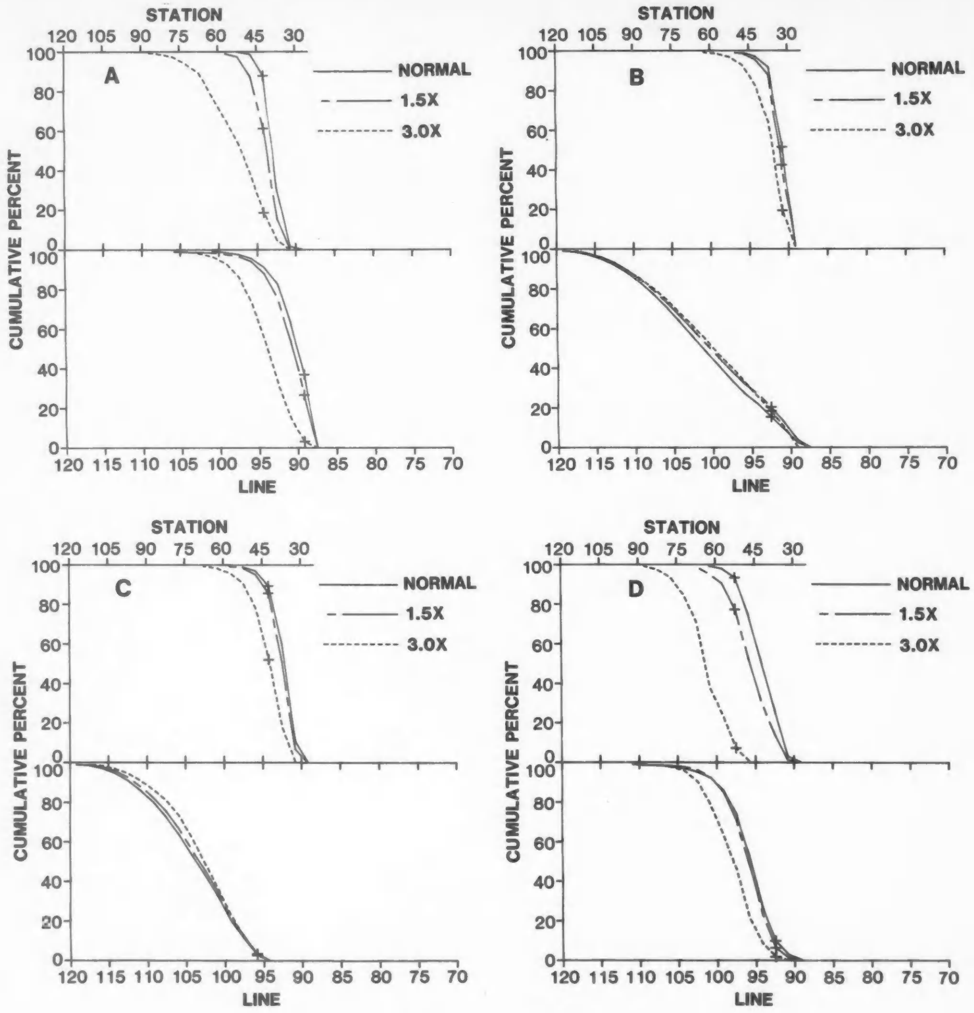
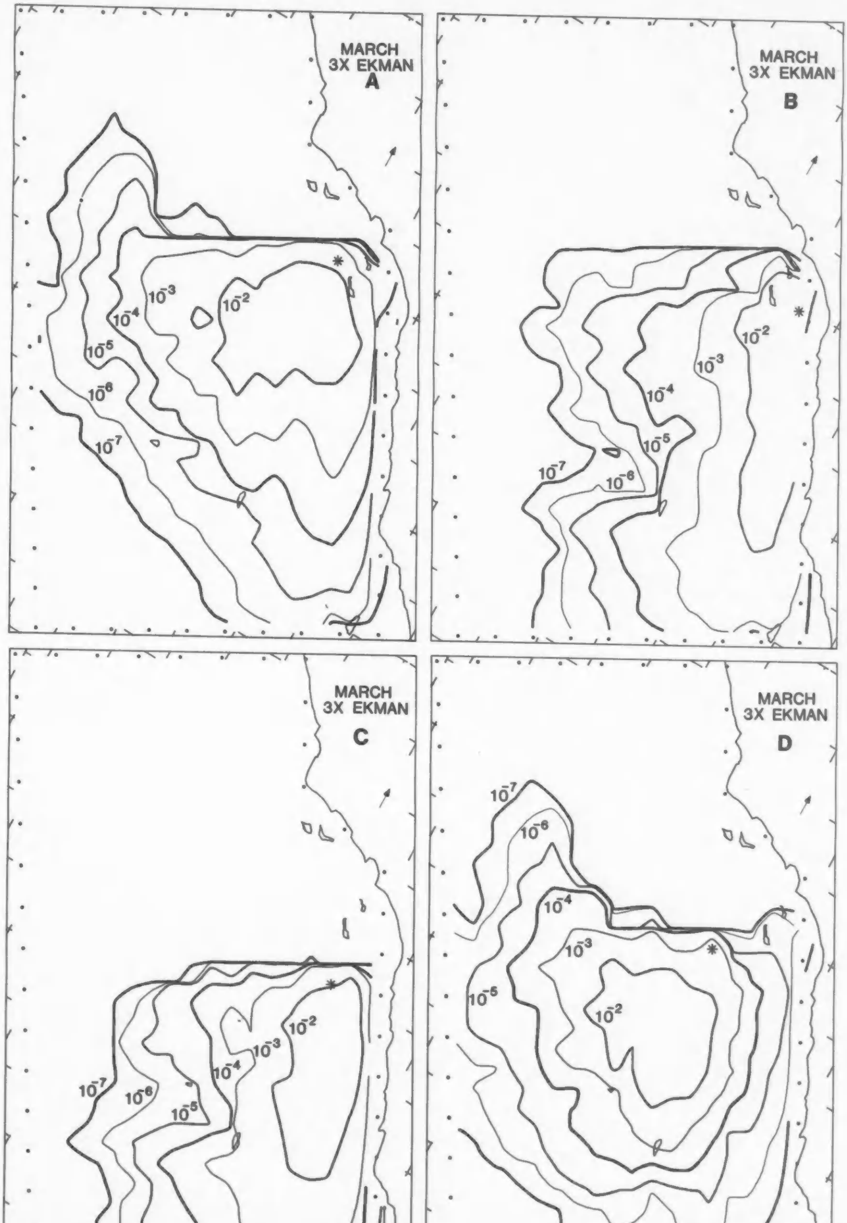


FIGURE 9.—Cumulative percentage plots of northern anchovy larval concentrations after 30 d drift in the three March Ekman current regimes ("normal" or long-term mean, 1.5× offshore directed Ekman transport, 3× offshore directed Ekman).

tions, and thus approximate what occurs in nature. The geostrophic current information, while some of the best available, nonetheless constrained the spatiotemporal resolution of this model, and incorporating Ekman transport required several assumptions. Further, there can be considerable interannual variability in the modeled region (Mooers and Robinson 1984; Simpson et al. 1984), and presumably the model is of "average" conditions and cannot be representative of any specific year; I felt that including such variability (assuming adequate data were available) would complicate the results without significantly contributing to biological insight. An

FIGURE 10.—Distribution of northern anchovy larvae after 30 d of drift in March currents with three times the normal offshore directed Ekman transport.


MARCH
3X EKMAN
A
10^{-2}
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MARCH
3X EKMAN
B
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
MARCH
3X EKMAN
C
10^{-2}
10^{-3}
10^{-4}
10^{-5}
10^{-6}
10^{-7}
MARCH
3X EKMAN
D
10^{-7}
10^{-6}
10^{-4}
10^{-3}
10^{-5}
10^{-2}

additional confounding factor is the lack of biological information in the model; consistent larval behavior patterns (e.g., diurnal vertical migrations) and spatially heterogeneous mortality could produce distributional patterns differing from those presented here. In spite of these caveats, the simulations do demonstrate that variations in northern anchovy spawning location and time, and changes in the magnitude of offshore directed Ekman transport, can have significant consequences for the subsequent larval distribution. By inference, these changes in distribution can result in increased or reduced larval mortality, and ultimately affect adult northern anchovy population size.

Offshore transport was not significant in the simulations done with the unaugmented or "normal" March (seasonal April geostrophic + March Ekman) currents. A majority of the northern anchovy larvae that began drift at the four starting locations were inshore of their starting points after 30 d of drift, and the cross-shore distributions indicated that most larvae occupied a relatively narrow range of distances close to shore. Mais (1974) and Methot (1981) reported that most juvenile northern anchovy occupy inshore areas in the fall, and the model indicates that this inshore movement could be facilitated by passive drift. As mentioned earlier, the consensus is that nearshore regions provide more hospitable food conditions for the northern anchovy larvae. Lasker (1978, 1981) summarized the results of surveys of larval food distributions in the Southern California Bight. His figures indicate that suitable larval food concentrations decline rapidly as one progresses offshore. O'Connell (1980) reported the results of a survey for starving northern anchovy larvae in the Southern California Bight, the degree of starvation being defined by histological criteria. He found apparently healthy larvae at locations as far as about 250 km offshore (at lat. 32°30′N, long. 120°W), where model concentrations were $<10^{-7}$ after 30 d in all March simulations except for larvae begun at A, where they were $<10^{-4}$. Despite the good condition of these offshore larvae, the simulation results indicate a low likelihood of their being recruited to the nearshore juvenile population. The low offshore larval concentrations will also hinder the development of schooling (Hewitt 1981a).

The minimal offshore transport situation found in the March current simulations was also generally true when simulations were done using currents from other seasons, except for northern anchovy larvae begun at location A. This point is the most interior starting location within the Southern California Bight proper and is primary northern anchovy spawning habitat (Hewitt 1980) and where seasonal changes in the currents are especially important (Tsuchiya 1980). Spring is a time when currents in the Southern California Bight are not as well organized as other times of the year, and the Southern California Eddy is often absent (Hickey 1979; Owen 1980). It is interesting that currents during March, the peak spawning period, produced the least offshore transport of larvae begun at location A when compared with other seasons, even though March is the time of greatest overall Ekman transport (Bakun and Nelson 1976). There is significant spawning in January (Methot 1981), and the January simulations also had reduced dispersal of larvae. The model results support the hypothesis of Parrish et al. (1981) that northern anchovy spawning in the Southern California Bight do so at a time and place that minimizes offshore transport of eggs and larvae.

It is clear that the overall 30-d alongshore distributions of northern anchovy larvae produced by normal March currents depended largely on the spawning location's proximity to the well-defined southeasterly current present near the coast in the southern half of the modeled region. Larvae that started drift near this current underwent extensive downshore transport. Larvae begun farther into the Southern California Bight (location A), and farther offshore (location D), were also transported downshore, but to a much lesser extent. This again confirms the role of the Southern California Bight as an area where minimal transport of spawning products takes place. The southwesterly, offshore transport that occurred in many of the simulations at the southern margin of the modeled region (between CalCOFI lines 110 and 120) is consistent with the evidence that this region forms a faunal boundary between species of the Southern California Bight and those of Baja California to the south, and that this faunal boundary is created by current patterns (Hewitt 1981b). This is also a region of increased surface convergence (Parrish et al. 1981).

The extent of alongshore transport was markedly different for northern anchovy larvae begun at the same starting location when currents from the different seasons were used. Depending on starting location, seasonal changes in currents could produce almost complete reversals between predominantly upshore or downshore transport. March currents consistently produced the greatest downshore transport. These effects were due to the presence or absence of the Southern California Eddy and the Southern California Countercurrent. Because the Southern California Countercurrent is present year-round, except during peak spawning in the spring, it is clear that the relationship between the time of northern anchovy spawning and the time that this countercurrent diminishes is critical. The simulations indicated that eggs and larvae from early spawning (i.e., January) are carried upshore into the Santa Barbara Channel and north of Point Conception, while those from later spawning (March) move in the opposite, southeasterly direction. The sizes and birth dates of juveniles collected in the fall of 1978 and 1979 were in accordance with this pattern. Methot (1981) reported that juvenile northern anchovy collected during both fall seasons in the northern portion of the Southern California Bight had birth dates (as determined from daily growth increments in otoliths) in the preceding months of December and January, and these fish were generally larger than those collected farther to the south. The northern anchovy collected in the south had predominantly February and March birth dates. It may be that the northern group, containing fish from early spawning, were advected to the north by the Southern California Countercurrent and that the southern group of fish from late spawning were produced when the surface countercurrent had diminished. Future studies of the transport and distribution of northern anchovy larvae or other planktonic species in the Southern California Bight should incorporate as much information as is available on the presence and magnitude of the Southern California Countercurrent and the Southern California Eddy.

Nearshore winds in the Southern California Bight are relatively weak, and downshore wind speeds generally increase farther offshore (Bakun and Nelson 1976; Nelson 1977; Dorman 1982). The implication, in terms of offshore transport, is that larvae closest to shore are affected least by offshore transport, while those farther offshore experience a much greater impact. Thus the areal extent of northern anchovy spawning interacts with offshore Ekman transport; in years when most northern anchovy spawn close to shore there will be decreased offshore transport, because of weak inshore winds, than in years when northern anchovy spawn farther offshore. The impact on the products of offshore spawning will depend on the magnitude of the winds in the offshore areas in each particular year. Northern anchovy larvae that began drift farthest north in the Southern California Bight (location A) and at the more offshore location (D) were most affected by increases in offshore directed Ekman transport, indicating southerly and inshore spawning are best for reduced dispersal in March. Hewitt and Methot (1982) stated that the area of northern anchovy spawning was more compact and more northerly in 1978 than in 1979. Survival of young larvae was about the same in both years, indicating that early mortality from starvation and predation was not substantially different in the two years. Survival through the juvenile stage was greater in 1978 than in 1979, however, and Hewitt and Methot (1982) cited increased offshore transport in 1979 as a possible reason.

Superimposed on the effects of spawning location is the interaction between the increase in downshore wind speeds (offshore directed Ekman transport) as one progresses offshore and the magnitude of interannual variations in the wind speeds. In the simulations the effects of the 3× increase in Ekman transport were substantially greater than those of the 1.5× increase. The 1.5× change was not a great enough increase to carry many northern anchovy larvae into offshore regions of higher, offshore directed Ekman transport. The inshore 3× increase carried a greater fraction of larvae farther offshore, and the 3× increase in the offshore region subsequently operated on a greater proportion of the larval population. Thus there was an interaction between enhanced offshore directed Ekman transport in the nearshore area and increased Ekman transport farther offshore, the two of these acting together to produce the extensive drift evident in the simulation results. Years in which downshore winds increase in only the inshore or the offshore regions would not produce as much overall offshore dispersal. Bakun and Nelson's (1976) statistical analyses of the "upwelling index" indicates that prolonged increased Ekman transport is feasible, although the 3× condition would probably be a particularly bad year. It should also be noted that Ekman transport was incorporated into the model as acting uniformly on the 50 m surface layer, and presumably the model depicts the drift of "average" larvae. Larvae that remain near the surface or at 50 m would undergo greater or lesser transport, respectively. Alternatively, it is known that winds in the Southern California Bight have a strong diurnal periodicity (Bakun and Nelson 1976; Dorman 1982), and a diurnal vertical migration coupled with diurnal changes in the winds could significantly alter larval drift.

In summary, the simulation results indicated that seaward dispersal of northern anchovy larvae is generally small, but that seasonal effects are strongest in the area of peak spawning (location A) and that March spawning at this point minimizes offshore dispersal. Spawning at locations or times near well-defined currents, such as the California Countercurrent, can produce major changes in larval distribution, and consequently may affect larval survival. The effect of offshore directed Ekman transport on the larval population depends on the areal extent of northern anchovy spawning, and the spatial distribution of any changes in wind stress and subsequent Ekman transport; an increase in Ekman transport in both the inshore and offshore regions will act together to produce maximum offshore dispersal.

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PARASITES OF BENTHIC AMPHIPODS: DINOFLAGELLATES (DUBOSCQUODINIDA: SYNDINIDAE)

PHYLLIS T. JOHNSON[1]

ABSTRACT

During a 2½-yr survey, 13 species of benthic amphipods collected from the continental shelf of the northeastern United States were found infected by dinoflagellates. Prevalences ranged from <1% to 67%, depending on amphipod species, time, and place of collection. The parasites are assigned to the order Duboscquodinida, family Syndinidae, based on similar life histories and a similar kind of mitosis ("mitose syndinienne"). Two types of organisms were involved, both apparently more closely related to *Hematodinium* Chatton and Poisson than to other described syndinids. Morphology and development of the parasites and host-parasite interactions are discussed. A cytochemical method used to determine presence or absence of basic nuclear proteins was strongly positive for basic proteins in spores and prespores but negative in most other stages. A few spores in four infections possessed a distinct flagellum, but in the absence of living material, shape of spores and whether they were biflagellate could not be determined. With three possible exceptions in the group of 303 infections studied, the syndinids were not recognized as foreign by their hosts, and in joint infections of syndinids and fungi, only the fungi were being attacked by host hemocytes. High prevalences in certain of the amphipod species suggest that the syndinids might be population regulators in these species.

This paper is one of three that describe and discuss the more common parasites found in populations of benthic amphipods of the continental shelf of the northeastern United States. The other papers concern microsporidans and ciliates (Johnson 1985, 1986).

Because my observations on the parasites discussed in this paper were based on examination of histological sections, I could not determine whether spores were typical "dinospores". However, agreement with other developmental stages of well-studied species of syndinids from copepods and an amphipod, and the nuclear type, indicates that the parasites of benthic amphipods are related to species currently placed in the Syndinidae, order Duboscquodinida (sensu Chatton 1952 and Cachon 1964). Previously described syndinids occur intracellularly in radiolarians and in copepod and shrimp eggs (Chatton 1952; Stickney 1978) and extracellularly in the hemocoel of copepods, an amphipod, and portunid and cancrid crabs (Chatton and Poisson 1931; Chatton 1952; Manier et al. 1971; Newman and Johnson 1975; MacLean and Ruddell 1978).

The relationship of the Duboscquodinida to free-living dinoflagellates is in doubt (Cachon 1964; Ris and Kubai 1974; Siebert and West 1974; Hollande 1975; Loeblich 1976; Herzog et al. 1984). Lacking a definitive consensus, the parasitic protists discussed here are provisionally referred to the Dinoflagellata.

The data presented and discussed in this paper show that species of syndinids are probably ubiquitous hemocoelic parasites of benthic and epibenthic amphipods, and may be population regulators in some species.

METHODS

The data are based on material collected during monitoring surveys carried out over a 2½-yr period by the Northeast Fisheries Center, National Marine Fisheries Service. The 35 stations where benthic amphipods were collected during the surveys are shown in Figure 1. Amphipods were sampled during 11 cruises, but not all stations were visited on each cruise, so that stations were sampled from 1 to 10 times each during the survey. A Smith-McIntyre[2] grab and occasionally an epibenthic sled or scallop dredge were used to obtain the samples. The 11 stations indicated by solid circles on Figure 1 had the most consistent and numerous populations of amphipods, and were sampled at least five times each. They yielded the majority of data presented here.

Amphipods were preserved in 10% seawater Formalin. Up to 30 individuals of each species pres-

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[1] Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Oxford, MD 21654.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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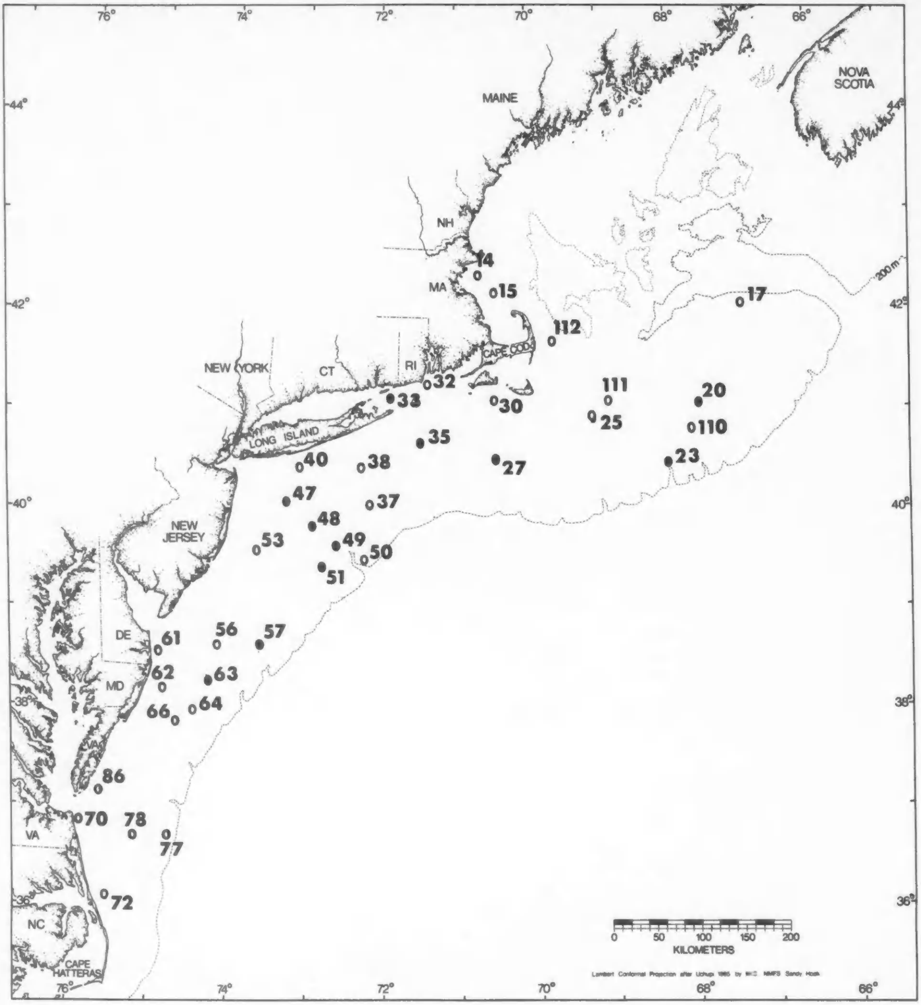
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FIGURE 1.—Benthic stations where gammaridean amphipods were sampled during the survey.

ent in a sample, and sometimes more, depending on numbers present, were prepared for histological study. Details of collecting procedures and histological preparation of the amphipods are given by Johnson (1985). Sections were cut at 6 μm. Staining methods included Harris' hematoxylin and eosin (H&E), the Feulgen reaction, and Alfert and Geschwind's (1953) fast-green method for demonstration of basic nuclear proteins. Harris' hematoxylin and eosin is specified because this combination stains nuclei of the parasites purple during certain stages. Other hematoxylin solutions, used with eosin, will not necessarily impart the same distinct purple color. Unless otherwise indicated, references to staining properties of the organisms are to H&E-stained specimens.

OBSERVATIONS

Thirteen amphipod species were infected with syndinids (Table 1). The organisms occupied the hemocoel and morphologically were most like *Hematodinium perezi* Chatton and Poisson, which was described from European portunid crabs. There were two distinct types, based on morphology and development. There is not enough information about the life history stages of *Hematodinium* to warrant assigning either or both types to that genus, and they are identified casually in this paper as "Type AA" and "Type AV" (Table 2). The Type AA forms were similar in all the amphipod species they infected, but there was variation in forms assigned to Type AV, and probably more than one species was involved.

Host and Geographic Distribution

Juvenile and mature amphipods of both sexes were attacked. Only Type AA was found in *Ampelisca agassizi* (Judd), *Byblis serrata* Smith, and

TABLE 1.—Amphipod species infected with Type AA and Type AV parasites.

Species of amphipod	Type of parasite	Prevalence positive stations (%)	Prevalence all stations (%)
Ampelisca agassizi (Judd)	AA	7 (101/1468)	4 (101/2403)
Byblis serrata Smith	AA	14 (24/170)	8 (24/316)
Harpinia propinqua Sars	AA[1]	18 (3/17)	3 (3/116)
Ampelisca vadorum Mills	AV	41 (74/181)	17 (74/448)
Ampelisca verrilli Mills	AV	18 (7/38)	15 (7/48)
Casco bigelowi (Blake)	AV	67 (6/9)	10 (6/60)
Leptocheirus pinguis (Stimpson)	AV	4 (7/163)	0.8 (7/913)
Melita dentata (Krøyer) *s. lat.*	AV	8 (1/12)	2 (1/44)
Monoculodes edwardsi Holmes	AV	27 (25/93)	23 (25/110)
Protohaustorius wigleyi Bousfield	AV	20 (1/5)	0.9 (1/110)
Phoxocephalus holbolli Krøyer	AV	27 (10/37)	14 (10/73)
Rhepoxynius epistomus (Shoemaker)	AA and AV	20 (7/35)	3 (7/249)
Unciola species (probably all *U. irrorata* Say and *U. inermis* Shoemaker)	AA and AV	9 (37/404)	3 (37/1365)

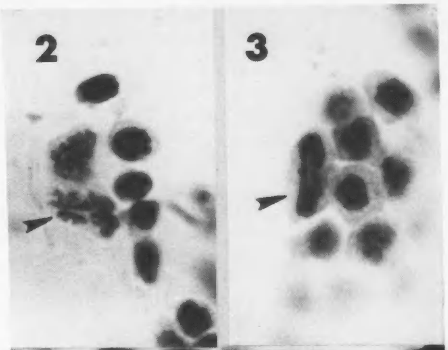
[1] Parasites in two of the infections may not be either Type AA or Type AV.

TABLE 2.—Main characteristics of Type AA and Type AV.

Stage	Characteristic	Type AA	Type AV
I	Nuclear diameter	<3 to >5 μm	2.5 to 3 μm
	Nuclear color	Blue or purple	Purple
	Chromosomes	Usually condensed	Not condensed
	Plasmodia	Present, small	Present, small
	Single cells	Common	Absent or uncommon
	Cytoplasm	Scanty	Abundant, faintly fibrous
IA	Dense bodies	Not present	Present, <2 μm in diameter
	Nuclear diameter	—	2.5 to 4 μm
	Nuclear color	—	Purple
	Plasmodia	—	Present, small
	Single cells	—	Present
II	Nuclear diameter	4 to 5.5 μm	3 to 4 μm
	Nuclear color	Purple	Purple
	Chromosomes	Indistinct, partly condensed	Distinct, partly condensed
	Plasmodia	Uncommon, small	Very rare
	Cytoplasm	Vacuolate	Homogeneous
III	Nuclear diameter (spore)	2.5 to 3 μm	<2 μm
	Nuclear color (spore)	Deep blue	Deep blue
	Chromosomes (spore)	Always condensed	Always condensed
	Cytoplasm (spore)	Scanty	Scanty
	Plasmodia	Absent	Present
	Nuclear diameter (plasmodia)	—	3.5 μm
	Nuclear color (plasmodia)	—	Purple

Harpinia propinqua Sars. Both Types AA and AV occurred in *Rhepoxynius epistomus* (Shoemaker) and *Unciola* species (*U. irrorata* Say and *U. inermis* Shoemaker), and only Type AV occurred in the remaining species (Table 1). Both types of syndinids were present in *Unciola* species taken in a single sample at station 35, but individual specimens were parasitized by only one type. There are not enough data to indicate whether or not incidence varies by time of year in any of the amphipod species infected with these parasites. Infected amphipods were not found at the most northern and southern of the stations, but these stations were sampled fewer times than most of the "positive" stations (i.e., stations where amphipods with syndinid infections occurred). There were 18 positive stations. Only Type AA was found at stations 23, 37, and 50. Only Type AV occurred at stations 33, 40, 56, and 62. Both types were represented at stations 20, 27, 35, 38, 47, 48, 49, 51, 57, 63, and 64.

Whether one or both types occurred at a single station depended variously on which amphipod species were present, and on unknown factors. Two species of *Ampelisca*, *A. vadorum* Mills and *A. agassizi*, were common at inshore station 33. Prevalence of Type AV in *A. vadorum* was 35% (56/158). However, Type AA did not occur at station 33 although a favored host, *A. agassizi*, was abundant there. In contrast, only Type AA was found at station 23, no doubt because of 2,811 amphipods collected there, only 23 were not *A. agassizi*.



FIGURES 2-3.—Mitosis in Type AV parasites in *Ampelisca vadorum* (arrowheads). Interphase parasites of Figure 3 are stage II.

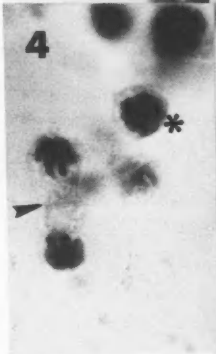


FIGURE 4.—Mitosis in a Type AA parasite in *Ampelisca agassizi* (arrowhead). Chromosomes form a rosette in the interphase nucleus to the right (asterisk).

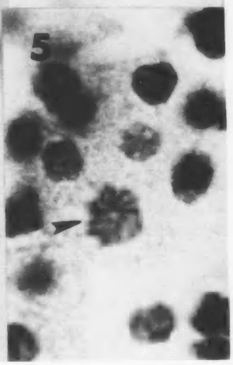


FIGURE 5.—Chromosomes in a lysed Type AA parasite from *Byblis serrata* (arrowhead). The V shape of the chromosomes is evident. Figures 2-5, × 1500.

Development and Morphology

All forms were similar in that extensive plasmodia were never present and chromosomes were condensed in the interphase nuclei of the spores. There were four, possibly five, chromosomes. There was no metaphase plate. At telophase the apices of the two sets of chromosomes were touching (see Figure 3), and at all stages of mitosis the chromosomes of each group were juxtaposed basally (where they presumably were attached to the nuclear membrane) and spread out apically to varying degrees, like the spokes of a parasol (Figs. 2-4). These events are typical of "mitose syndinienne" (Chatton 1921). Syndinid chromosomes are V-shaped, so that each has two arms. In tissue sections the V shape was best seen in cells that had lysed, leaving only the chromosomes (Fig. 5). During telophase there were often only four (sometimes five?) visible arms of chromosomes in each daughter nucleus. If sectioning artifact was not responsible for the small number of visible arms, the cells might have been haploid.

Before spore formation, chromatin disposition in nuclei was variable, depending on the type of parasite and the stage of development. Resting nuclei with unfolded chromosomes were granular or vesicular, and sometimes rimmed with chromatin (see Figures 8, 17). In nuclei with partially unfolded chromosomes, clumps of chromatin often were arranged so that they created a dashed or dotted line in the position that would be occupied by a completely condensed chromosome (see Figure 9). When seen in a polar view, chromosomes or chromatin clumps formed rosettes (Figs. 4, 5). Morphology of the persistent chromosomes of spores was variable and will be described later.

Staining characteristics of nuclei differed depending on the stage. Except for spores, prespores, and some cells in early Type AA infections, nuclei tended to be purple, not blue, with both chromatin and the matrix staining similarly in some cases. When nuclei at these stages were in mitosis, the chromosomes were little, if at all, bluer than chromatin in resting cells, although sometimes chromatin was more deeply staining in the dividing cells. Types of chromosomes that stained with fast green by the Alfert and Geschwind method (indicating presence of basic proteins on the chromosomes) would stain blue in H&E preparations. Chromatin and chromosomes that did not stain with fast green in the Alfert and Geschwind method would stain purple with H&E.

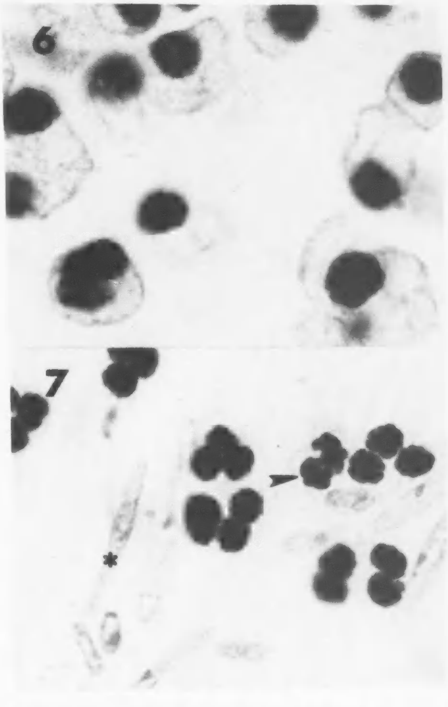
A comparison of Types AA and AV, by developmental stage, is given in Table 2. Infections consisting of few parasites were considered to be the earliest ones and are here designated stage I infections. Stage II infections consisted of more numerous and generally larger organisms, and stage III infections consisted of prespores and spores that usually filled the hemocoel.

Type AA

Most Type AA infections were in *Ampelisca agassizi* (Table 1). Type AA chromosomes of all developmental stages were usually thicker than those of Type AV (compare Figures 2 and 4), and the organisms and their nuclei were larger (Table 2). Stage I organisms were scattered through the hemocoel, never numerous, and variable in morphology and staining characteristics. The one common attribute was scanty and poorly staining cytoplasm. Chromosomes were usually distinct. The most usual stage I infection consisted of scattered single cells and small plasmodia with nuclei that measured 3 to 4 μm and had rather distinct chromosomes or chromatin clumps that stained a clear blue. Mitotic figures were not frequent, but were more common than in the other stages. A few cells in a late stage I (or very early stage II) infection probably were polyploid. They had many rather long, tangled chromosomes that sometimes formed partially separated groups within the nuclear area. The nuclei of these cells measured more than 7 μm in the greater dimension.

Stage II organisms were more numerous and distinguished by having voluminous vacuolate or foamy cytoplasm (Fig. 6). Chromosomes and chromatin clumps were often obscured because the nuclear matrix stained almost as strong a purple as the chromatin. The nuclear matrix did not stain in the Feulgen reaction. Plasmodia were uncommon, always small, and sometimes consisted of short chains of joined cells. Mitosis was rarely seen in stage II and stage III, and probably was closely synchronized, which would reduce the probability of finding mitotic figures in fixed material. As the spore stage was approached, nuclei became smaller and bluer, and chromatin clumps and chromosomes gained clear outlines, because the matrix no longer stained.

By the time of spore formation (stage III), organisms filled the hemocoel, and infected amphipods in H&E-stained sections could be distinguished with the naked eye because of their overall dark-blue color. Spore nuclei were spherical, and chromosomes were condensed but tightly packed and impossible to count (Fig. 7). In one infection, synchronized nuclear division had apparently just taken place, and daughter cells had not yet separated, so that bi- and



FIGURES 6-7.—Type AA parasites in *Ampelisca agassizi*. 6: Stage II. Nuclei do not have distinct clumps of chromatin and the cytoplasm is vacuolate. 7: Stage III (spores) (arrowhead). An unidentified fungus was also infecting the amphipod (asterisk). Figures 6-7, × 1500.

quadrinucleate plasmodia were common. Cytoplasm of spores was scant. Sometimes spores were shaped like teardrops but generally they had amorphous outlines. A flagellum was visible on a few spores in an individual of *Unciola* species.

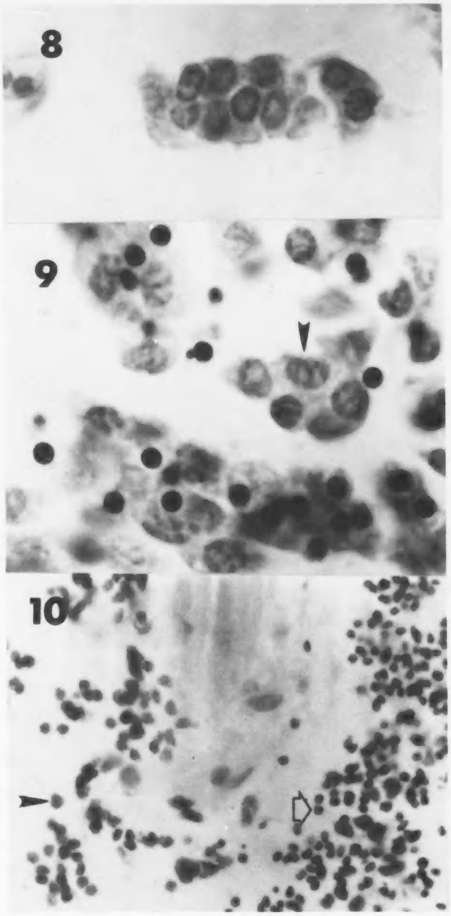
Type AV

This description is based on the organisms that infected *Ampelisca vadorum*. Stage I consisted of scarce and scattered small plasmodia, typically each with 2 to 10 nuclei. Their cytoplasm was faintly fibrous. Chromatin and the nuclear matrix were always purplish and nuclei were often rimmed with chromatin (Fig. 8). The nuclear matrix was not Feulgen positive, and chromatin did not stain strongly by this method. Slightly more advanced infections, with more parasites, had irregularly shaped single cells as well as plasmodia. The single organisms were often elongate, their nuclei were as above, and their cytoplasm was faintly stained.

Stage IA, which I presume follows stage I, and which did not occur in Type AA, had moderate numbers of small plasmodia and single cells. Chromatin patterns were rather distinct in most nuclei, particularly in the larger ones. Chromatin stained purple. Stage IA was distinguished by the presence of small, densely staining bodies. They were usually spherical but sometimes oval, and were usually surrounded by thin rims of cytoplasm. The bodies were associated with the plasmodia (Fig. 9) and also scattered through the hemocoel. They were intensely Feulgen positive and stained bright green by the Alfert and Geschwind method. The dense bodies were never extremely abundant and were present only in the company of many stage IA cells.

Chromosomes of stage II cells were partially condensed, and chromosomes and chromatin clumps were distinct because there was minimal staining in the nuclear matrix, unlike Type AA parasites in stage II. The cytoplasm was usually densely and homogeneously stained (Fig. 3). Cells were often very numerous and closely packed, but were not plasmodial. Occasionally there were a few dense bodies like those associated with stage IA.

Occasional stage III infections were not as heavy as some stage II infections. There was apparently an abrupt transition from stage II cells to stage III prespores and spores. In one infection, a mass of spores with distinct deep-blue chromosomes occupied a circumscribed area in the hemocoel, and larger single cells with condensed chromosomes that stained purple, and were probably very late stage II, occupied the remainder of the hemocoel (Fig. 10). Presumably, the mass of spores resulted from synchronized but circumscribed division of a part of the population of the larger cell type. The roughly spherical nuclei of the spores in this infection were <2 μm in diameter; nuclei of the larger cells were slightly >3 μm in diameter.

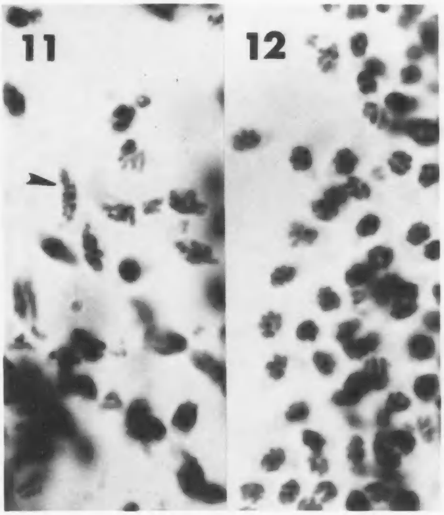


FIGURES 8-10.—Type AV parasites in *Ampelisca vadorum*. 8: Stage I. Several nuclei in the plasmodia are rimmed with chromatin. 9: Stage IA. Plasmodia with associated spherical dense bodies. Nuclei are pale and chromosomes are partially unfolded in some nuclei (arrowhead). 10: Late Stage II (larger, pale nuclei to the left—arrowhead) and Stage III (smaller, deeply staining nuclei to the right—open arrow). A demonstration of synchronized division of the parasite. Larger host nuclei are also present. Figures 8-9, × 1500; Figure 10, × 600.

Cells presumed to represent spores had either elongate or spherical nuclei (Figs. 11, 12). The two types did not occur together. Mitosis took place in very small cells, and possibly cells with spherical nuclei were prespores. They might also have been spores that had not yet acquired their final form, because cells of an intermediate shape also occurred. Chromosomes of the spherical nuclei were short; those of elongate nuclei were longer, somewhat more slender, and beaded. Because the cytoplasm was usually indistinct or invisible, outlines of spores were also indistinct. It is probable that spores often ruptured during fixation, resulting in loss of all cell components except the chromosomes, as shown in Figure 11.

A probable polyploid cell was present in one early stage III infection, and there were small plasmodia in all stage III infections (as in Figure 17). Nuclei in plasmodia had purple-staining chromatin and did not stain by the Alfert and Geschwind method, unlike chromosomes of the spores. The relationship of the small plasmodia to spore formation was not obvious.

Numbers of Type AV-infected individuals of species other than *A. vadorum* and *M. edwardsi* were small, and all stages of development were not usually represented. Stage IA infections, as well as some or all the other stages, were seen in *Ampelisca verrilli* Mills, *Leptocheirus pinguis* (Stimpson), *Casco bigelowi* (Blake), and *Unciola* species. Stage IA infections of *A. verrilli* and *C. bigelowi* differed from those of *A. vadorum* because the small dense bodies were often irregularly shaped or composed of two or three contiguous particles rather than being single and spherical or oval. In one of two stage III infections in *L. pinguis*, spores had almost spherical chromosomes (Fig. 13). In the other, chromosomes were indistinct because they were closely packed, but were longer than in the first infection and apparently beaded. All stages of infection were represented in *Unciola* species. Spore nuclei were round or oval and a flagellum was visible on a few spores in two infections. The final divisions were just taking place in one of these infections, and many cells were still binucleate. Most of the single spores had rounded outlines, but spores with a visible flagellum were oval.

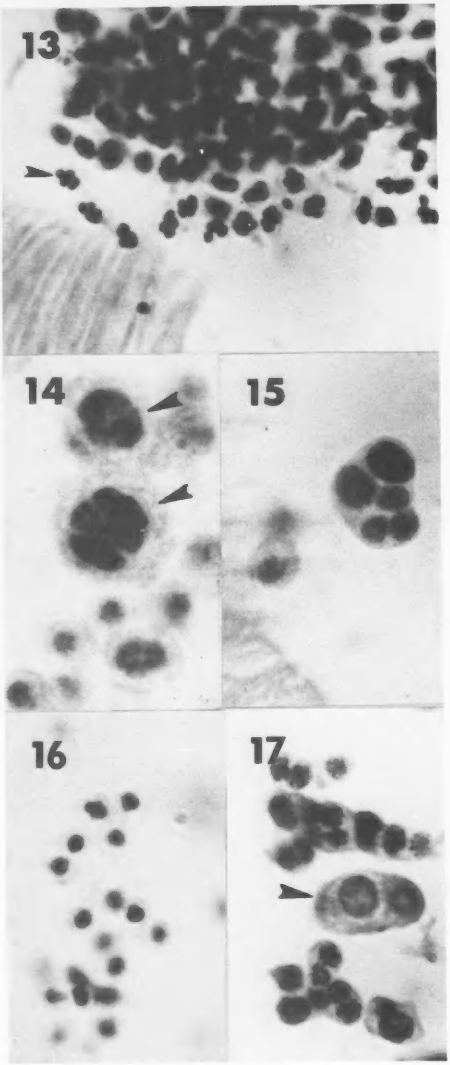


FIGURES 11-12.—Type AV, Stage III (spores), in *Ampelisca vadorum*. 11: Elongate spores. Note the beaded appearance of the chromosomes in one spore (arrowhead). 12: Spherical spores. Figures 11-12, × 1500.

Monoculodes edwardsi had the highest overall prevalence of Type AV (Table 1). The 25 infections encompassed all stages except Stage IA. There were polyploid cells in stage II infections. Their nuclei were sometimes over 6 μm in diameter, often had chromatin separated into several areas (Fig. 14), and their chromosomes were seldom completely condensed, except in mitotic cells. Polyploid cells in mitosis had at least three sets of chromosomes. Outlines of both the interphase nucleus and the entire cell were often highly irregular. Plasmodia that presumably resulted from nuclear division of the polyploid cells often had nuclei of two or more sizes (Fig. 15), suggesting that all chromosome sets did not divide at the same time, or that the genetic material was not distributed equally at the time of division, so that a single plasmodium might have contained haploid, diploid, and polyploid nuclei. Nuclei of Type AV spores in *M. edwardsi* were about 1 μm in diameter (Fig. 16). A single flagellum (not pictured) was visible on some spores in the infection presented in Figure 16. As typical of Type AV, plasmodia were present in all stage III infections (Fig. 17).

Host Response

Reactions against the syndinid parasites were extremely rare. One Type AV-infected specimen each of *Melita dentata* (Krøyer) *s. lat.* and *Unciola* species had scattered, melanized, amorphous nodules in the hemocoel, but the nodules could not be definitely associated with the syndinid infections. In one specimen of *L. pinguis*, hemocytes were associated



FIGURES 13-17.—Type AV parasites. 13: Stage III (spores) in *Leptocheirus pinguis*. The chromosomes are spherical (arrowhead). 14: Stage II in *Monoculodes edwardsi*. Two of the parasites are polyploid (arrowheads). Note separate groups of chromosomes or chromatin clumps in both these parasites. 15: Plasmodium resulting from nuclear division of a polyploid parasite in *M. edwardsi*. Note differently sized nuclei. 16: Stage III (spores) in *M. edwardsi*. There were flagellated spores in this infection. 17: Prespores, some dividing, in *M. edwardsi*. A plasmodium, with rimmed nuclei, is also present (arrowhead). Figures 13-17, × 1500.

with Type AV organisms, and karyorrhexis had occurred in unidentified cells in the area. With the possible exception of the Type AV infection in *L. pinguis*, the syndinids were not being attacked by hemocytes at the time of fixation.

There was another sign that the syndinid parasites successfully evaded detection by their hosts. Two specimens of *A. agassizi*, both collected at station 47 but at different times, were infected jointly and heavily with Type AA and an unidentified fungus (Fig. 7). Of the more than 7,000 examined microscopically, these were the only two amphipods that had systemic fungal infections. Fungi were being phagocytized by hemocytes and fixed phagocytes, and other groups of fungi were being transformed into melanized nodules. (Probably the latter fungi had originally been phagocytized and killed by hemocytes that did not survive the process themselves.) Although hemocytes and fixed phagocytes were actively destroying fungi, there was no indication that the accompanying syndinids were recognized as foreign.

Numbers of hemocytes apparently decreased during syndinid infection, but even in heavy infections some hemocytes remained and were still functional as shown by their ability to phagocytize the fungi discussed above. It is probable that the two successful fungal infections in syndinid-infected amphipods resulted in part from the fungi multiplying more rapidly than they could be phagocytized and degraded by the few remaining hemocytes and the fixed phagocytes associated with the heart.

The syndinid parasites did not castrate their hosts.

Whether death ensues from every infection with these parasites is not known. However, the general lack of discernible host response makes it unlikely that amphipods could successfully combat the parasites.

DISCUSSION

Like species of *Syndinium* described from copepods, Types AA and AV have a small number of chromosomes which are permanently condensed in spores and partially condensed in certain other stages; plasmodia (small and multiple in the case of Types AA and AV) are present during some developmental stages; and spore formation takes place in the hemocoel of the host. However, species of *Syndinium* in copepods differ from Types AA and AV in that they develop from a plasmodium that is first applied to the wall of the gut and then expands to fill the entire hemocoel. The massive plasmodium then fragments to form individual dinospores. By the time of sporulation, the host is castrated (Chatton 1910, 1920). Types AA and AV resemble *Hematodinium*, not *Syndinium*, in that apparently none of these organisms develop from a primary plasmodium associated with the gut, but instead they multiply from a few single cells and small plasmodia in the general hemocoel and never form a single massive plasmodium. Further, these parasites do not castrate their hosts (Newman and Johnson 1975; MacLean and Ruddell 1978; P. T. Johnson, unpubl. data).

Syndinium gammari, like Types AA and AV, is perhaps more closely related to *Hematodinium* than to *Syndinium*. *Syndinium gammari* was assigned to *Syndinium* by Manier et al. (1971) on the assumption that a massive plasmodium was present during development. However, none of the infections studied by these authors had either a primary plasmodium associated with the gut or a later and massive plasmodium throughout the hemocoel. The first stage of *S. gammari* observed consisted of small irregular plasmodia up to 15 μm in diameter, which Manier and coworkers assumed resulted from the splitting-up of a large plasmodium. The small plasmodia then divided to form "diplococcal" forms, and these divided to give round, single organisms which transformed into spores measuring 7-8 μm by 3-3.5 μm. In the later stages of division, typical "dinomitosis" and "dinokaryons" were present. Considering the course of development in the apparently related parasites of benthic amphipods, Types AA and AV, it is possible that *S. gammari* does not have a primary plasmodium associated with the gut wall and does not develop an extensive plasmodium in the hemocoel. If early stages of *S. gammari* consist of a few single cells or small plasmodia, these could have escaped notice because the parasites were observed after their removal from the host amphipod, either alive or in fixed and stained smears (Manier et al. 1971). Scattered organisms could more easily be missed by this technique than by inspection of paraffin-embedded and sectioned whole amphipods.

Chromosomes of *Solenodinium globiforme* and three species of *Syndinium*, all parasites of radiolarians, stain with fast green in the Alfert and Geschwind method for demonstration of basic nuclear proteins (Ris and Kubai 1974; Hollande 1975). Ris and Kubai remarked that chromosomes of the *Syndinium* species they studied also stained brightly in the Feulgen reaction. Although not definitely stated by the above authors, apparently chromosomes of all developmental stages of the above parasites stained equally with fast green. Chromosomes of these species tend to remain condensed through the entire developmental cycle. On the other hand, Hollande (1975) found that trophont nuclei of the duboscquodinids *Amoebophrya ceratii* and *Duboscquella melo* do not stain by the Alfert and Geschwind method. He pointed out that chromosomes are not condensed in the trophont nuclei of these forms and that he did not investigate staining properties of the condensed chromosomes of spores. Hollande did find that a portion of the nucleolus of *A. ceratii* stains with fast green in the Alfert and Geschwind method. Like the syndinid parasites of radiolarians, chromosomes of Type AA and AV spores stain brightly in both Alfert and Geschwind's technique and the Feulgen reaction. However, Feulgen staining is less intense in stages I and II nuclei and these nuclei do not stain at all with fast green.

Eukaryotes have a greater quantity of histone in rapidly dividing cells than in quiescent ones (DuPraw 1968; Wu et al. 1982), and nonhistone basic nuclear proteins—although scarce at all times—are much more abundant in log-phase than in stationary-phase cultures of the free-living dinoflagellates *Gyrodinium cohnii* and *Peridinium trochoideum* (Rizzo and Noodén 1974). It would be interesting to determine the relative amounts of basic nuclear proteins through the developmental cycle of syndinids and other duboscquodinids, and to determine whether basic proteins of the amphipod parasites increase when cells are dividing rapidly; and whether these proteins are masked by other substances (acidic proteins?) in stages where both chromatin and nuclear matrix stain purple with H&E and do not stain in the Alfert and Geschwind method.

Probably fixation and paraffin embedment not only damaged flagella and were responsible for apparent lack of flagella on most spores of Types AA and AV, but also distorted spores of these parasites. Cachon (1964) cautioned that because spores of parasitic dinoflagellates become distorted or ruptured both on fixation and when physical conditions are not proper, their shapes must be determined in living material.

Origin and function of the small dense bodies present in Type AV, stage IA infections were not evident. These bodies might represent necrotic nuclei like those seen in *Syndinium* infections (Jepps 1936-37), discarded chromatin resulting from reduction divisions, or, perhaps, nuclei of microspores (Cachon 1964).

Numbers of *Gammarus locusta* (Linn.) infected with *Syndinium gammari* in the Étang de Thau, France, varied from few to all members of a population (Manier et al. 1971). The infected amphipods these authors examined were apparently unaffected by the parasite. However, before one could determine the mortality rate due to syndinid infection, it would be necessary to examine moribund and dead amphipods found in the field for presence of syndinids, as well as to follow progress of infection in the laboratory. Syndinids appear to be unaffected by host defense mechanisms. Spores of syndinids that parasitize the hemocoel must exit through breaks in the exoskeleton or gut. Because hemocytes are in short supply by time of sporulation and other host resources can be expected to be depleted, host defense mechanisms probably would not be sufficient to prevent death by infection with other microorganisms that would enter through the breaks or death by leakage of body fluids. Assuming, on the basis of evidence presented in this paper, that amphipods are unable to contain syndinid infections and that most infections would therefore progress to the spore stage, syndinid infection could serve as a population regulator in heavily parasitized species. *Monoculodes edwardsi* and *Ampelisca vadorum*, which had overall prevalences of syndinid infection of 23% and 17% respectively, are examples of species that might be affected in this manner.

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FOOD HABITS AND DIET OVERLAP OF TWO CONGENERIC SPECIES, *ATHERESTHES STOMIAS* and *ATHERESTHES EVERMANNI*, IN THE EASTERN BERING SEA

M. S. YANG[1] AND P. A. LIVINGSTON[2]

ABSTRACT

Stomachs of 196 arrowtooth flounder, *Atheresthes stomias*, and 152 Kamchatka flounder, *A. evermanni*, collected from the same area of the eastern Bering Sea in summer 1983 were examined. Each species was divided into four fork-length groups: less than 201 mm, 201-300 mm, 301-400 mm, and greater than 400 mm. The principle diet of both species was comprised of walleye pollock, *Theragra chalcogramma*, shrimp (mostly Crangonidae), and euphausiids. Pollock was the most important prey item for both species in all four size groups, ranging from 56 to 86% and 66 to 88% of the total stomach content weight of Kamchatka flounder and arrowtooth flounder, respectively. Schoener's indices of diet overlap were calculated between the two species for each size group. The high value of the indices (ranging from 0.67 to 0.90) indicate that these two congeneric species basically consume the same resources.

The genus *Atheresthes* of the family Pleuronectidae has two species: Kamchatka flounder, *A. evermanni* (Jordan and Starks), and arrowtooth flounder (Norman, 1934), *A. stomias* (Jordan and Gilbert). *Atheresthes evermanni* is distributed from northern Japan (Hokkaido) through the Sea of Okhotsk to the western Bering Sea north to Anadyr Gulf (Willimovsky et al. 1967). *Atheresthes stomias* is distributed from Central California to the eastern Bering Sea. In the Bering Sea, it meets about on a line with Saint Matthew Island, overlaps with, and is replaced by *A. evermanni* (Hart 1973).

Because the morphological differences between *A. evermanni* and *A. stomias* are subtle, they have been recorded as one species, *A. stomias*, in the eastern Bering Sea resource assessment surveys of the Northwest and Alaska Fisheries Center (NWAFC) (Smith and Bakkala 1982). Food habits of *A. stomias* have been studied by some researchers (Gotshall 1969; Kabata and Forrester 1974; Smith et al. 1978), but none of those studies covered the food habits of *A. evermanni*. Shuntov (1970) studied the feeding intensity of the two *Atheresthes* species, but he did not compare the diets of these species.

Using electrophoretic examination, Ranck et al. (1986) have confirmed that these two types of *Atheresthes* are separate species. The purpose of this study is to analyze stomach samples of these two congeneric species collected in the area of their distributional overlap in the eastern Bering Sea and compare the diets of both fish species to calculate the degree of diet similarity to determine whether the two species can be considered trophically equivalent.

COLLECTION AND PROCESSING OF SAMPLES

Specimens were collected from 6 July to 16 July 1983 in the eastern Bering Sea aboard the *Alaska*, a research vessel participating in the annual summer resource assessment survey conducted by the Resource Assessment and Conservation Engineering (RACE) division of the NWAFC in Seattle, WA. Stomachs of arrowtooth flounder and Kamchatka flounder were taken at standard resource assessment stations where half-hour tows were made using an 83-112 Eastern bottom trawl net with an estimated 2.3 m vertical and 16.4 m horizontal mouth opening.

The samples were collected in an area around and to the northwest of the Pribilof Islands at bottom depths ranging from 71 to 137 m (Fig. 1, Table 1). A random subsample of individuals of both arrowtooth flounder and Kamchatka flounder was obtained at each station with a total collection of 348 stomachs from 19 stations.

Individual fish were first checked for signs of regurgitation, i.e., food items in mouth or gill plates or flaccid stomach, and were discarded if any such signs were noted. Stomachs from the remaining fish

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[1] Fisheries Research Institute, University of Washington, WH-10, Seattle, WA 98195.

[2] Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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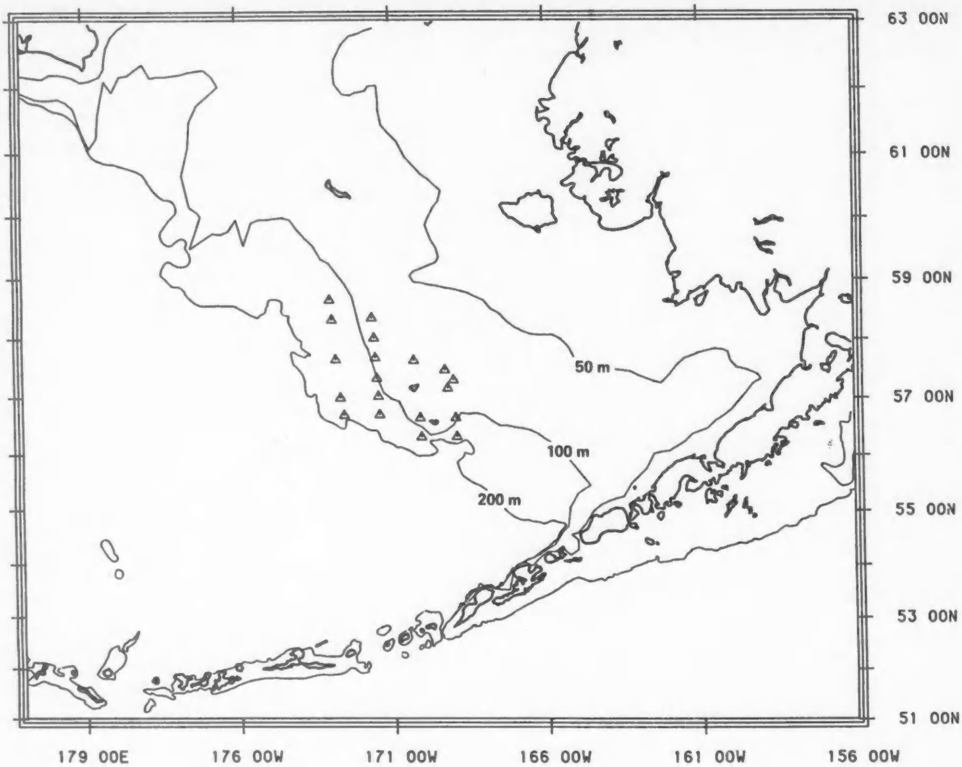

FIGURE 1.—Sampling locations for arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*, in summer 1983 in the eastern Bering Sea.

were excised along with the anterior portion of the body (including head, stomach, and intestines), and these samples were sent to the laboratory for species identification. Each specimen was placed in a muslin bag with a specimen label bearing fork length, sex, and station information. All samples were preserved in 10% Formalin[3].

In the laboratory, two characters were used for species identification: the position of the left eye relative to the dorsal profile and gill rakers. Kamchatka flounder has the upper eye completely on the right side of the head and 13 or fewer gill rakers on the first arch. Arrowtooth flounder has an upper eye which interrupts the dorsal profile of the head and 15 or more gill rakers on the first arch (Norman 1934; Willimovsky et al. 1967).

Stomachs were analyzed individually. Prey items were identified to the lowest taxonomic level practical, counted, and weighed damp to the nearest milligram. The standard length of fish prey were also measured.

DATA ANALYSIS

Specimens of *A. stomias* and *A. evermanni* were divided into 100 mm fork-length groups for data analysis: <201 mm, 201-300 mm, 301-400 mm, and >400 mm. Percent of frequency of occurrence (% FO), percentage of total stomach content weight (% W), percentage of total prey number (% N) and the Index of Relative Importance [IRI = % FO (% N + % W)] (Pinkas et al. 1971) were calculated for major categories of prey items in the 100 mm size groupings of *A. stomias* and *A. evermanni*.

Based on a review of dietary overlap measures

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Station information and number of stomachs collected at each station of arrowtooth flounder (ATF) and Kamchatka flounder (KF) in the eastern Bering Sea for the summer 1983.

Haul	Date	Alaska daylight time	Haul depth (m)	Bottom temp. (°C)	Latitude N	Longitude W	No. ATF[1] stomachs collected	No. KF[1] stomachs collected
100	7/6	1000	71.3	3.1	56°29.46′	169°15.61′	14 (6)	19 (17)
101	7/6	1200	71.3	3.1	57°19.25′	168°59.13′	4 (5)	2 (1)
102	7/6	1400	76.8	2.6	57°10.87′	169°10.22′	14 (6)	7 (6)
105	7/7	0800	102.4	2.7	56°39.96′	168°55.22′	18 (9)	7 (4)
106	7/7	1100	133.5	3.8	56°20.18′	168°53.24′	11 (2)	10 (3)
107	7/7	1600	111.6	3.5	58°20.01′	170°02.15′	12 (0)	12 (1)
108	7/8	0800	96.9	3.8	56°40.00′	170°04.47′	5 (1)	3 (1)
114	7/9	1400	75.0	2.7	57°39.23′	170°16.12′	13 (1)	2 (0)
135	7/13	1900	96.9	1.5	58°22.09′	171°37.39′	6 (1)	0 (0)
136	7/14	0700	100.6	2.8	58°01.90′	171°33.37′	5 (0)	1 (0)
137	7/14	1000	100.6	3.0	57°41.94′	171°31.16′	7 (0)	0 (1)
138	7/14	1300	102.4	3.7	57°21.05′	171°28.26′	8 (3)	6 (1)
139	7/14	1500	109.7	3.9	57°02.54′	171°25.63′	11 (0)	6 (1)
140	7/14	1800	120.7	3.7	56°43.42′	171°23.38′	6 (0)	9 (0)
141	7/15	0700	137.2	4.0	56°42.72′	172°32.33′	2 (6)	7 (2)
142	7/15	0900	124.4	3.6	57°00.84′	172°39.37′	5 (6)	7 (2)
144	7/15	1500	122.5	3.7	57°40.10′	172°47.92′	3 (1)	2 (0)
146	7/16	0600	111.6	2.6	58°20.10′	172°55.00′	2 (2)	9 (0)
147	7/16	0900	115.2	2.6	58°40.07′	172°59.18′	3 (0)	3 (0)
Total							149 (47)	112 (40)

[1] Stomachs containing food, number of empties in parentheses.

(Cailliet and Barry 1979; Linton et al. 1981), Schoener's (1970) index was chosen because it was found to measure overlap accurately over most of the range of potential overlap (Linton et al. 1981). Schoener's index, *Cxy*, is calculated as

$$Cxy = 1.0 - 0.5\left(\Sigma\left|p_{x,i} - p_{y,i}\right|\right)$$

where $p_{x,i}$ and $p_{y,i}$ are the estimated proportions by weight of prey i in the diets of species x and y, respectively (the percentage by weight of prey items in Table 2). The index ranges from 0 which indicates no dietary overlap to a maximum overlap of 1 when all prey items are found in equal proportions.

RESULTS

General Feeding Trends

A total of 348 stomachs were analyzed; 87 stomachs (25%) were empty. Table 2 shows the percentages by weight of all prey items found in the stomachs of both flounder species by size group. In general, both species consumed the same prey species or groups: euphausiids, pandalid and crangonid shrimps, and walleye pollock (Fig. 2). *Thysanoessa inermis* and *T. raschii* were the dominant euphausiids consumed. Some pandalid shrimps were eaten by smaller (<301 mm) flounders of both species, but crangonid shrimps, mainly *Crangon communis*, were the dominant shrimp consumed. Walleye pollock constituted the highest proportion of the diet for all size groups of flounder, ranging from 56% by weight of the diet for Kamchatka flounders 301-400 mm long to about 88% by weight for arrowtooth flounders >400 mm long. Miscellaneous food items consumed included polychaetes, copepods, cumaceans, hippolytid shrimps, ophiuroids, and various fish species.

Mean stomach content weight of those stomachs with food was similar between arrowtooth flounder and Kamchatka flounder for all but the largest size group. The mean stomach content weight ranged from about 1.4 g for the small flounders to over 20 g for the largest size group.

Diet Comparisons Within Size Groups

The principle diet of both *Atheresthes* species in the ≤200 mm size group was comprised of walleye pollock, euphausiids, and shrimps (Fig. 3). Walleye pollock comprised 58% and 65.5% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively. Euphausiids comprised the highest percentage by numbers of the diet of both species, 53% for Kamchatka flounder and 69.4% for arrowtooth flounder. Shrimps, including *Crangon communis*, *Pandalus goniurus*, *Pandalus tridens*, and *Eualus avinus*, constituted 17.1% and 7.2% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively. Other less important

TABLE 2.—Percentage by weight of prey items in the stomachs of arrowtooth flounder (ATF) and Kamchatka flounder (KF) by 100 mm FL categories; and Schoener's indices (*Cxy*) of diet overlap between the two species.

	Predator size group (mm)							
	≤200		201-300		301-400		>400	
Prey item	KF	ATF	KF	ATF	KF	ATF	KF	ATF
Invertebrates								
Polychaeta	—	—	—	0.28	—	—	—	—
Copepoda	—	0.01	—	—	—	—	—	—
Mysidacea	0.45	0.34	0.12	—	—	—	—	—
Cumacea	—	—	0.01	—	—	—	—	—
Amphipoda	0.22	—	0.52	—	0.07	—	—	—
Euphausiiacea								
Unidentified	5.64	8.99	0.23	9.10	0.54	3.86	—	0.22
Thysanoessa rachii	—	2.76	—	1.35	—	2.32	—	—
T. inermis	4.28	10.67	3.55	9.33	7.40	10.03	4.09	6.55
Caridea								
Unidentified	1.05	1.31	—	—	—	0.08	—	—
Hippolytidae								
Eualus avinus	0.88	—	—	0.05	—	—	—	—
Pandalidae								
Unidentified	—	1.08	—	—	—	—	—	—
Pandalus goniurus	3.89	—	—	—	—	—	—	—
Pandalus tridens	4.77	—	—	—	—	—	—	—
Pandalus sp.	0.54	0.37	0.24	—	—	—	—	—
Crangonidae								
Unidentified	0.34	2.98	2.15	0.10	—	—	0.07	—
Crangon dalli	—	—	0.85	0.61	—	—	—	—
C. communis	5.67	1.43	5.53	0.70	0.31	0.15	—	0.22
Paguridae	—	0.01	—	—	0.58	—	—	—
Ophiuroidea	—	0.19	—	—	0.03	—	—	—
Chaetognatha								
Sagitta sp.	—	0.03	—	0.01	—	—	—	—
Pisces								
Gadidae								
Unidentified	—	—	5.40	4.62	2.70	5.65	8.20	—
Theragra chalcogramma	58.03	65.51	81.55	71.69	55.78	76.99	85.87	87.96
Zoarcidae								
Unidentified	—	—	—	—	5.55	—	—	5.06
Lycodes brevipes	—	—	—	—	8.20	—	—	—
Cottidae	—	1.15	—	—	—	—	—	—
Stichaeidae								
Unidentified	3.00	—	—	—	—	—	—	—
Lumpenus maculatus	—	3.16	—	1.97	9.47	—	—	—
Pleuronectidae								
Unidentified	7.50	—	—	—	9.36	—	1.77	—
Atheresthes sp.	3.73	—	—	—	—	—	—	—
Unidentified organic material	—	—	0.05	0.19	—	0.92	—	—
No. of stomachs with food	32	40	43	53	20	40	19	14
Total weight of stomach content (g)	46.96	57.24	93.29	167.66	181.89	291.43	383.32	467.91
Mean stomach content weight (g)	1.47	1.43	2.17	3.16	9.09	7.29	20.17	33.42
Mean fish length (mm)	187.80	184.60	250.10	260.70	350.50	341.30	441.10	450.00
Cxy	0.72		0.82		0.67		0.90	

food items were stichaeids, pleuronectids, cottids, mysids, and amphipods.

Walleye pollock, the dominant food of both *Atheresthes* species in the 201-300 mm size group (Fig. 3), constituted 81.6% and 71.7% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively. Euphausiids comprised 20% by weight of the diet of arrowtooth flounder. However, euphausiids only comprised 3.8% by weight (39.9% by number) of the diet of Kamchatka flounder. Shrimps (Crangonidae, Pandalidae) were more important food for Kamchatka flounder (8.8% by weight) than for arrowtooth (1.4% by weight). Unidentified gadoids comprised 5.4% and 4.6% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively. Other less important food items were polychaetes, mysids, amphipods, and the stichaeid *Lumpenus maculatus*; they were

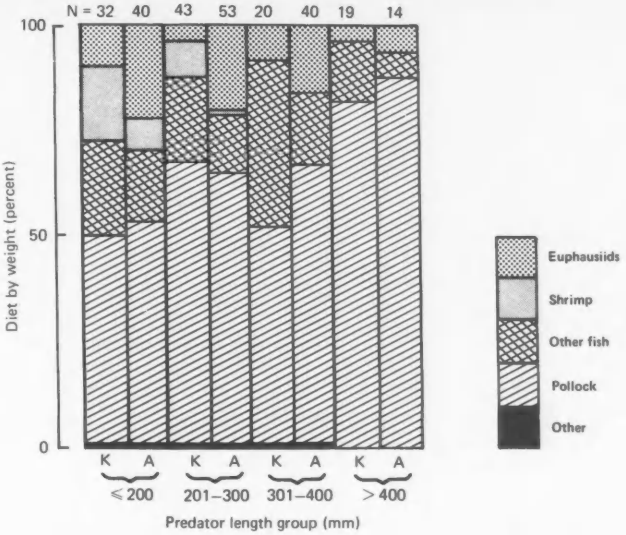

FIGURE 2.—Percentage by weight of major prey categories in the diet of arrowtooth flounder (A), *Atheresthes stomias*, and Kamchatka flounder (K), *A. evermanni*, for different length groups of fish collected from the eastern Bering Sea in summer 1983.

all <5% by weight of the diet of both *Atheresthes* species.

The principle diet by weight of Kamchatka flounder in the 301-400 mm size group was comprised of 55.8% walleye pollock, 13.8% zoarcids, 9.4% pleuronectids, 9.5% stichaeids, and 7.9% euphausiids (Table 2, Fig. 3). Walleye pollock also dominated the diet of arrowtooth flounder (77% by weight). The other two main items of arrowtooth flounder were euphausiids (16.2% by weight) and unidentified gadoids (5.7% by weight). Shrimps were not important food for either *Atheresthes* species of this size; they contributed <1% by weight of the diet. Other less important prey items were ophiuroids and pagurids. Numerically, euphausiids dominated the food for both species (90.7% for Kamchatka flounder, 96.0% for arrowtooth flounder).

Walleye pollock dominated the food of the two *Atheresthes* species in the >400 mm size group (Fig. 3). It constituted 85.9% and 88.0% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively (Table 2). Though euphausiids dominated the food by number (91.5% for Kamchatka flounder, 97.0% for arrowtooth flounder), they only contributed 4.1% and 6.8% by weight of the diet of Kamchatka flounder and arrowtooth flounder, respectively. In addition to walleye pollock, unidentified gadoids comprised 8.2% and pleuronectids comprised 1.8% by weight of the diet of Kamchatka flounder. Zoarcids comprised 5.1% by weight of the diet of arrowtooth flounder. Shrimps played a less important role in the food of both *Atheresthes* species (<1% by weight).

Diet Comparison Among Size Groups

There was not much difference in diets among size groups in the proportion by weight of the prey categories such as euphausiids and fish (Fig. 2). However, shrimps disappeared from the diets of flounders in the two larger size groups. The number of different species in the diet also changes with size. The ≤200 mm size group of flounders consumed about 11 or 12 different prey categories while the >400 mm size groups consumed only 3 or 4 different prey types (see Table 2).

Even though the proportion by weight of fish in the diet remained fairly constant over flounder size groups, the size of individual fish consumed did change with flounder length. Figure 4 shows the frequency distribution of fish prey lengths found in the stomachs of different size *A. evermanni*. Most of the prey fish were age-0 juvenile pollock (<100 mm) for the two smaller size groups and age-1 juvenile

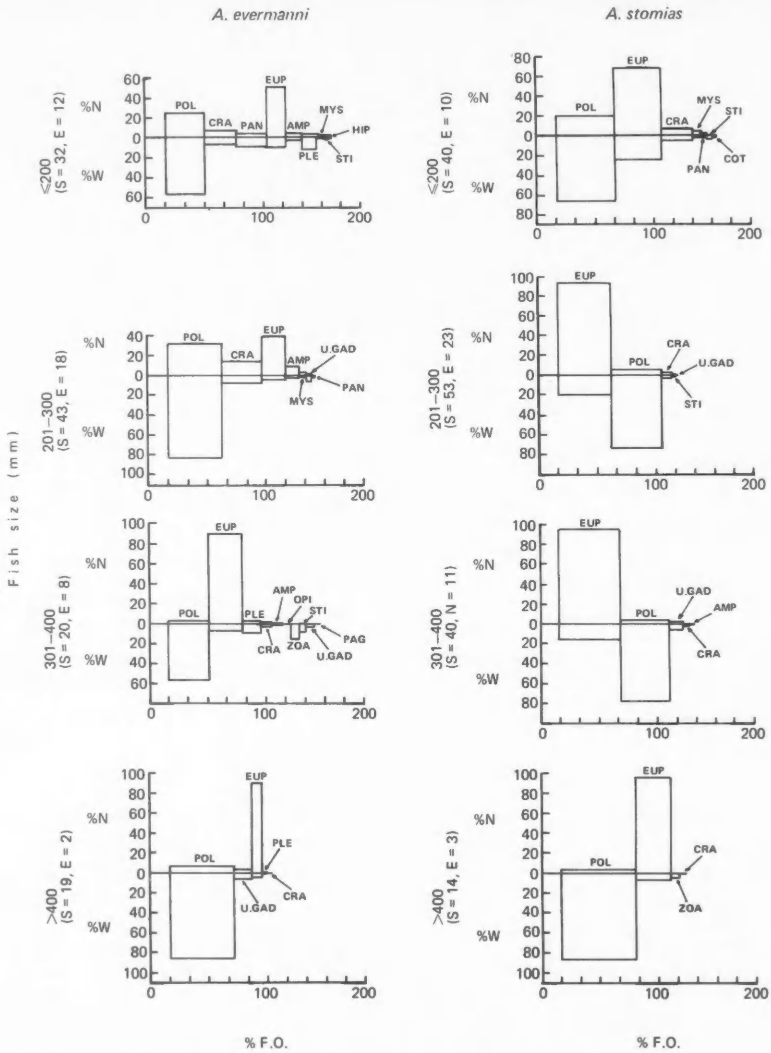

FIGURE 3.—Indices of Relative Importance of major prey items in the diets of *Atheresthes evermanni* and *A. stomias* of different size groups. % F.O., percent frequency of occurrence; % N, percentage of prey number; % W, percentage of total stomach content weight; POL, pollock; EUP, Euphausiacea; CRA, Crangonidae; PAN, Pandalidae; AMP, Amphipoda; PLE, Pleuronectidae; MYS, Mysidacea; STI, Stichaeidae; HIP, Hippolytidae; ZOA, Zoarcidae; U. GAD, Unidentified Gadidae; COT, Cottidae; S, number of stomachs containing food; E, number of empty stomachs.

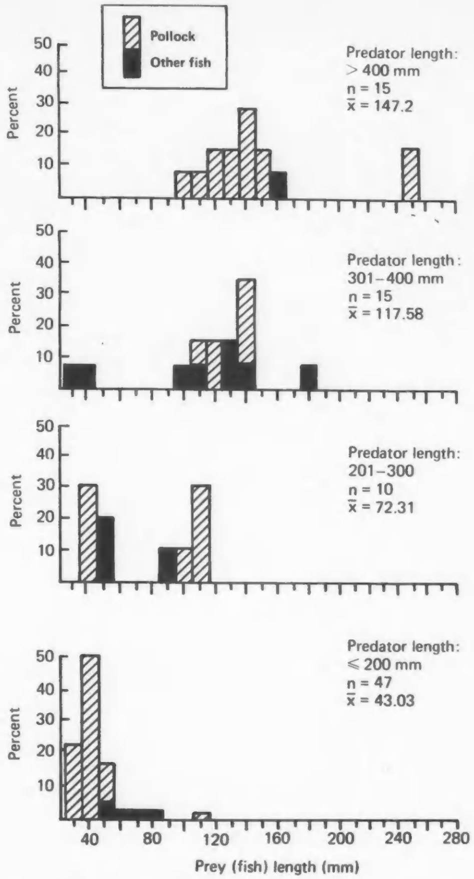

FIGURE 4.—Frequency distribution of standard lengths of prey fish found in the stomachs of *Atheresthes* species from the eastern Bering Sea in summer 1983.

pollock (100-200 mm) for the two larger size groups. The fish prey length was plotted against the predator length (Fig. 5). Fish prey size appears to increase linearly with increasing predator size.

Diet Overlap

Values for Schoener's (1970) index of dietary overlap were obtained from a comparison (by weight) between the diets of Kamchatka and arrowtooth flounder of the same size groups (Table 2). All the values obtained were >0.60, an indicator of high dietary overlap (Langton 1982). The ≤200 mm size group had an overlap value of 0.72 and the 201-300 mm size group had an overlap value 0.82. Within each of these two size groups, fairly similar proportions by weight of walleye pollock, euphausiids, and shrimps were consumed. The 301-400 mm size group had the lowest overlap value of 0.67. This is probably because Kamchatka flounder ate less walleye pollock by weight (56%) than did the arrowtooth flounder (77%). Most of the remainder of the diet for Kamchatka flounder in this size group was composed of different fish groups, such as zoarcids, stichaeids, and pleuronectids, which were almost totally absent from the arrowtooth's diet at this size. The largest size group of flounders (>400 mm) had the highest overlap value of 0.90. This size group ate very similar proportions by weight of walleye pollock and euphausiids.

DISCUSSION

From this study, it appears that both Kamchatka flounder and arrowtooth flounder are largely fish feeders. Walleye pollock was the most frequently observed prey and contributed the largest percentage by weight to the diets, followed by euphausiids and shrimps (Table 2, Fig. 3). Gotshall (1969) found that ocean shrimp, *Pandalus jordani*, was the most common food item of arrowtooth flounder (because the stomachs were collected on commercial shrimp grounds), followed by fishes and euphausiids. Pacific sanddabs, *Citharichthys sordidus*, were the most numerous prey fish found in his study. Kabata and Forrester (1974) examined 753 arrowtooth flounder collected off the west coast of Vancouver Island. Their study showed that euphausiids, followed by fish were the predominant foods taken by arrowtooth flounder. The most commonly found species of fish were eulachon, *Thaleichthys pacificus*, and Pacific herring, *Clupea pallasii*. Smith et al. (1978) found that fish constituted 41.09% and euphausiids 37.22% by volume of the food of 236 arrowtooth flounder collected from the northeast Gulf of Alaska. Walleye pollock were most commonly consumed fish prey. Moiseev (1953) found that Kamchatka flounder fed almost exclusively on pollock and only occasionally on herring and other fishes.

The type of prey eaten by a fish is strongly correlated with the morphology of the alimentary tract of the fish (De Groot 1971; Ebeling and Cailliet 1974; Allen 1982). Structure of the digestive tract of arrowtooth flounder and Kamchatka flounder are very similar. Both have a very large terminal mouth that is nearly symmetrical with a wide gape; teeth are arrow-shaped and well developed on both sides of the jaws; gill rakers are long and strongly dentate;

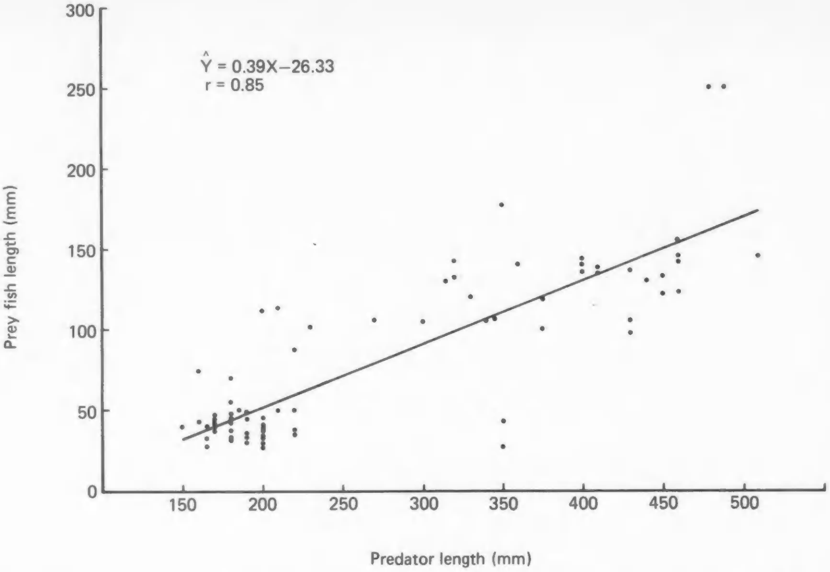

FIGURE 5.—Scatter plot of prey fish length consumed by *Atheresthes* species from the eastern Bering Sea in summer 1983.

and the esophagus and stomach are large with four large pyloric caeca and the intestine is a simple loop. All of these characteristics indicate that *Atheresthes* species are fish feeders as predicted by using De Groot's (1971) morphological criteria. He stated that large gill rakers with teeth are indispensable to fish feeders, since they prevent the prey, grasped alive, from struggling out of the mouth. The high percentages of fish in the diet of the two *Atheresthes* species obtained in this study would be expected on the basis of the similarities in the digestive tracts of the two species.

The results also indicate that *Atheresthes* species feed up in the water column. According to Allen (1982), flatfishes with large symmetrical mouths (*Atheresthes* species) probably use sight to locate prey. They are oriented up in the water column when foraging. The presence of pelagic fish (*T. chalcogramma*) and euphausiids or nektonic benthopelagic crustaceans such as shrimps in the diets of *Atheresthes* species supports Allen's generalizations concerning correlations between morphology and feeding behavior in flatfishes.

The trend of the feeding habits of *Atheresthes* species with regard to predator length is toward piscivory; that is, when the predators are bigger, they take more fish (by weight) as food. Specimens from the ≤200 mm size group were found to ingest the greatest variety of prey items in comparison to other size groups. Specimens >400 mm long preyed mainly on other fishes, primarily on pollock. However, euphausiids were of importance in the diet of all size groups. One 460 mm arrowtooth flounder was found to have 838 *Thysanoessa inermis* in its stomach. Smith et al. (1978) also noted a change in food habits with increasing length in the arrowtooth flounder. In their study, specimens over 450 mm long preyed exclusively on pollock and other gadoids. Euphausiids were important food of the arrowtooth flounder up to 350 mm long; however, none were found among the stomach contents of specimens larger than 350 mm.

Based on the results of this study and those of Smith et al. (1978) and Gotshall (1969), it appears that *Atheresthes* species are opportunistic feeders; they feed on those prey items that are most abundant—pollock and euphausiids in the Gulf of Alaska and eastern Bering Sea and ocean shrimp in northern California. In the eastern Bering Sea, the estimated abundance of age-0 pollock in 1982 is between 100 billion and 1,300 billion and, based on the results of the 1983 bottom trawl survey by NWAFC, this 1982 year class is the largest observed since the large 1978 year class (Traynor in press).

In spite of the high diet overlap between Kamchatka flounder and arrowtooth flounder, there is probably no competition for food between these two species because they are exploiting abundant food sources.

Finally, although Kamchatka founder and arrowtooth flounder are genetically distinct, they can be considered trophically equivalent on the basis of their similar diets and high diet overlap.

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ECOLOGY OF CERIANTHARIA (COELENTERATA, ANTHOZOA) OF THE NORTHWEST ATLANTIC FROM CAPE HATTERAS TO NOVA SCOTIA

ANDREW N. SHEPARD,[1] ROGER B. THEROUX,[2] RICHARD A. COOPER,[1]
AND JOSEPH R. UZMANN[2]

ABSTRACT

Ceriantharia, tube dwelling anthozoans, were collected in grab samples and documented by direct observations and photographs from research submersibles on the continental shelf and slope off the northeast United States coast (Cape Hatteras to Nova Scotia). Two species [(*Cerianthus borealis* Verrill and *Ceriantheopsis americanus* (Agassiz)] were identified from grab samples and four species, probably including *C. borealis*, were observed from submersibles.

Ceriantharia distribution in relation to latitude, depth, temperature, and sediments was examined. They occurred throughout the study area, abundantly at depths of 0 to 500 m and less abundantly from 900 to 2,400 m. Ceriantharia habitats displayed an extreme range in bottom water temperature (summer maximum minus winter minimum) of from 8° to 16°C, and had every sediment type, except 100% gravel and coarse shifting sand. Geographic and bathymetric zonation is attributed primarily to temperature and secondarily to food supply and substrate type.

Ceriantharia distribution patterns, in submarine canyon heads at depths of <400 m, were determined from photographic transects run with submersibles; observed patchiness may be related to local differences in food supply, sediments, and microtopography.

The motile megafauna associated with Ceriantharia "forest" areas and the infauna and epifauna inhabiting ceriantharian tubes were evidence to show that tubes may enhance local species diversity and abundance in featureless soft-bottom areas by 1) attracting motile species seeking cover and 2), acting as a stable, elevated substrate for tubiculous and suspension feeding macrofauna.

The possibility of exploitation of energy reserves beneath the northwest Atlantic outer continental shelf and slope has prompted many new studies and the reexamination of past investigations for baseline information on the region's seafloor communities. Research submersible studies of potential oil lease tracts identified "indicator species" for assessing environmental changes owing to drilling activities. We considered Ceriantharia suitable for this purpose because they were abundant, passive suspension feeders, and nonmobile. Literature searches revealed that very little has been published on the Ceriantharia species occurring from Cape Hatteras to Nova Scotia. This is surprising in light of the group's significant contribution to the benthic biomass of the region (Wigley and Theroux 1981) and the important functional role [the effect a species has on the distribution and abundance of other residents (Sutherland 1978)] Ceriantharia may have in structuring communities inhabiting featureless soft-bottom substrate (O'Connor et al. 1977).

Woods Hole Laboratory, Northeast Fisheries Center (NEFC), National Marine Fisheries Service (NMFS), personnel have reported on the general composition and distribution of invertebrate fauna of the New England and Mid-Atlantic Bight continental shelf and slope (e.g., Wigley and Theroux 1981; Theroux and Wigley 1984[3]; Cooper et al., in press). Data on Ceriantharia were collected during ecological studies pertaining to various kinds of demersal fishes and benthic invertebrates: 1) a grab sample survey (Fig. 1) done from 1955 to 1969 (Shepard and Theroux 1983[4]), and 2) observations, photographs, and limited sample collections from research submersible studies. Dredge and trawl data were available (Shepard and Theroux fn. 4), but not analyzed since deep burrowing Ceriantharia (some-

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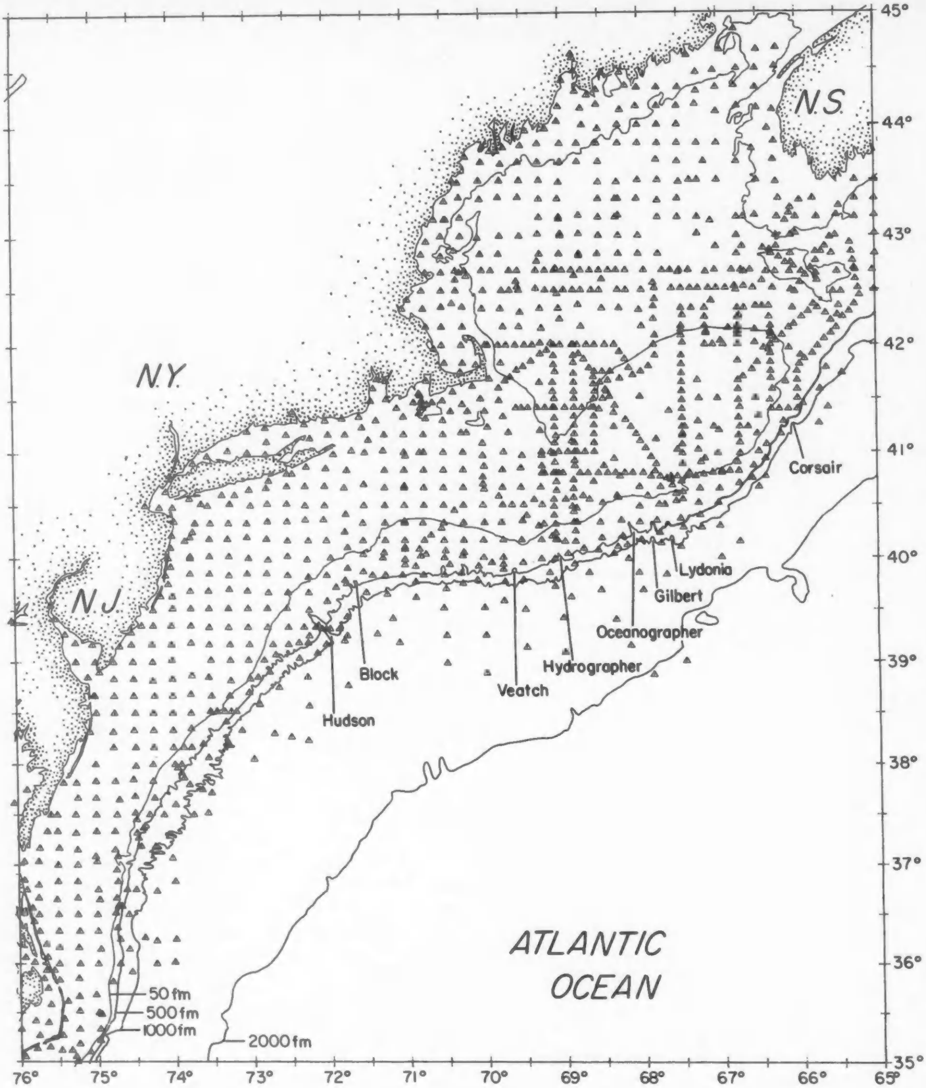
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Oceanographer
Hydrographer
Veatch
Block
Hudson
ATLANTIC
OCEAN
50 fm
500 fm
1000 fm
2000 fm

FIGURE 1.—Chart of the northwest Atlantic from lat. 35° to 45°N (Cape Hatteras to Nova Scotia) showing stations where grab samples of macrobenthic invertebrates were obtained, and the location of submarine canyons visited with research submersibles (1 fm = 1.83 m).

times more than 1 m; Sebens[5]) may be poorly sampled by dragged collection gear.

The objectives of this study are to describe 1) the Ceriantharia species encountered, 2) their general distribution in relation to latitude, depth, temperature, and sediments, 3) their local distribution patterns, and 4) how they interact with other benthic species.

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CERIANTHARIA

Cerianthanians represent a small, incompletely described order of Anthozoa. Species identification is difficult, and many species probably remain undescribed since twice as many larval forms as adults are known (Hartog 1977; Hartog[6]). Two northwest Atlantic species have been identified; *Cerianthus borealis* Verrill (1873) (see also Parker 1900; Kingsley 1904; Widersten 1976) and *Ceriantheopsis americanus* (Agassiz 1859) (see also Verrill 1864; McMurrich 1890; Parker 1900; Carlgren 1912; Field 1949; Widersten 1976). Two other unidentified species have been found on the continental slope (Grassle et al. 1975; Hecker et al. 1980; Valentine et al. 1980; Sebens in press). Table 1 summarizes the geographic and bathymetric ranges of the above four species.

Ceriantharia live in permanent semirigid tubes composed of a type of cnidae peculiar to the Order (called ptychocysts by Mariscal et al. 1977), mucus, and adhering substrate debris (Emig et al. 1972). The feltlike tube is usually deep purple in coloration and distinct enough to be used alone as evidence of Ceriantharia presence. New England bottom trawl fishermen are familiar with nets fouled with cerianthanian tubes (Rogers 1979). In contrast to other burrowing anemones which have a single whorl of tentacles, Ceriantharia have two distinct whorls (marginal and oral tentacles) which remain outside the tube during feeding and rapidly retract into the tube when disturbed.

Ceriantharia are protandric hermaphrodites; gametes are produced in the mesenteries and fertilization is external. The larvae are pelagic and duration of the planktonic stage is variable (Carlgren 1912; Hyman 1940; Robson 1966; TRIGOM-PARC 1974). Adults are capable of oral disc regeneration by budding (Hyman 1940; Frey 1970). Asexual reproduction has been described for at least one species, *Aracnanthus oligopodus* (Cerfontaine 1909).

Ceriantharia are carnivorous passive suspension or impingement feeders (Emig et al. 1972; Caracciola and Steimle 1983). Digestion may begin in the tentacles, and larger particles are primarily taken up in the endoderm of sterile septa (Tiffon and Daireaux 1974). Fish species inhabiting the region, including cod, haddock, flounder, scup, and skate are known predators of whole juvenile Ceriantharia (Bowman and Michaels[7]) and may graze the tentacles of adults (TRIGOM-PARC 1974). Off the U.S. west coast, a nudibranch, *Dendronotus iris* Cooper, preys on adult Ceriantharia (Wobber 1970).

Previous documentation of Ceriantharia in the northwest Atlantic has come from grab samples (Sanders 1956; Wigley 1968; Pearce 1972; Pearce et al. 1976; Pearce et al. 1981; Reid et al. 1981; Wigley and Theroux 1981; Caracciola and Steimle 1983) and submersibles (Grassle et al. 1975; Rowe et al. 1975; Hecker et al. 1980; Valentine et al. 1980). However, no studies in the region report exclusively on cerianthanian ecology.

TABLE 1.—Morphologic descriptions and geographic and bathymetric ranges of previously described Ceriantharia species inhabiting the study area.

Species	General morphologic description	Geographic range	Bathymetric range (m)
Ceriantheopsis americanus	see Verrill 1864	Cape Cod to Florida[1]	[2]0-[3]70
Cerianthus borealis	see Verrill 1873	Arctic to Cape Hatteras[1]	10-[4]500
Unidentified species I[5]	small (<5 cm contracted), dark brown tentacles, tube flush to seafloor.[5]	Continental slope off New England	[5,6,7]>1,000
Cerianthid A[8]	larger than unidentified species I, uniformly dark tentacles, tube flush to seafloor[5]	Continental slope off New England	[5,6,7,8]>1,500

[1] Parker 1900.
[2] Field 1949.
[3] Pearce et al. 1981.
[4] Miner 1950, p. 196.
[5] Sebens in press.
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METHODS

Grab sample methodology (gear description, sample processing, data reduction, bathymetry, temperature, and sediments) is reported in Wigley and Theroux (1981). A chi-square (χ^2) test, employing contingency tables (Richmond 1964), was used to assess ceriantharian occurrence at grab sample stations (relation to latitude, depth, bottom water temperature, and sediment type).

Table 2 lists the submersibles used and sampling gear employed by each. Quantitative data were obtained with externally mounted 35 mm camera-strobe systems. Qualitative ecological and behavioral information was acquired with 35 mm hand-held cameras, audio tapes, and video tapes made with a hand-held or externally mounted video camera. In situ faunal and sediment collections were made with the submersibles' manipulator arms. Only those dives performed to assess the distribution of megabenthos and associated habitat types were analyzed.

The externally mounted 35 mm camera systems used on *Nekton Gamma*, *Johnson-Sea-Link*, and *Alvin* were quantitatively calibrated, assessing 3.6 m^2, 7.0 m^2, and 15.0 m^2 of ocean floor per photographic frame, respectively (Bland et al. 1976; Cooper and Uzmann 1981[8]).

Photographs were read on either a light table with a hand-held magnifying glass or motorized microfilm reader with a 36 × 36 cm screen and 15× magnification lens. Each photograph was time-annotated, thus allowing correlation with depth, temperature, slope angle, substrate-habitat type, and current speed and direction documented on hand-held audio recorders during the dives.

TABLE 2.—Submersible, cruise year, and gear used for data collection. PC8 = *Perry Model C8*, NG = *Nekton Gamma*, AL = *Alvin*, and JSL = *Johnson-Sea-Link*.

Submersible/ year	Audio tapes	Video tapes	35 mm photographs		In situ collections of fauna/ substrate
			Hand-held	External	
PC8/1971	X	X			
NG/1973	X	X	X		
NG/1974	X	X	X		
NG/1979	X	X		X	
AL/1975	X	X		X	X
AL/1976	X	X			X
AL/1978	X	X			X
AL/1980	X	X		X	X
JSL/1980	X	X		X	X
JSL/1981	X	X		X	X

RESULTS

Species Identification

Ceriantharia occurred at 229 of the 1,295 grab sample stations; 990 anemones were caught at 139 stations, whole tubes only at 29 stations, and tube fragments at 61 stations (Fig. 2). Two species, *Ceriantheopsis americanus* and *Cerianthus borealis*, were identified from grab samples (at four stations), the remaining anemones were identified only as Ceriantharia. The mean blotted wet weight of the 990 anemones was 5.0 g (95% C.L. = ±3.6); however, more than 90% weighed less than the mean.

Ceriantharia occurred at 82% of the submersible dive sites (Appendix Tables 1, 2) and at every major geographic feature visited (Fig. 2, Table 3). Submersible samples have not yet yielded anemones suitable for identification to the species level. Figure 3 shows three of the four species (Cerianthids A, B, C, and D) photographed from submersibles, and Table 3 classifies the species by morphological features apparent in photographs.

The minimum gross Ceriantharia size (height above seafloor or width of exposed tentacle crown and/or tube) visible in photographs was about 5 cm. It was not unusual to see large Cerianthid B or C tubes 20 cm above the seafloor. Based on laboratory examination of 61 anemones and a few specimens which were photographed in situ and then collected with the manipulator arm, a gross size of 5 cm corresponds to an anemone wet weight of about 16 g (3 times the mean weight of anemones captured with grab samplers).

Relation to Latitude

Ceriantharia occurrence at grab sample stations was not independent of latitude (χ^2, $P < 0.05$). Occurrence was highest in three areas: off Chesapeake Bay (lat. 37° to 38°N); south of Cape Cod in the zone also including the southern half of Georges Bank (lat. 40° to 41°N); and on the shelf off Nova Scotia (lat. 44° to 45°N) (Fig. 4).

From submersibles, Cerianthid B was the only species seen on Georges Bank, or north of 41°N [Wilkinson Basin (Gulf of Maine) and Corsair Canyon]; Cerianthids A, C, and D were all seen in canyons or on the slope south of Georges Bank (Table 3).

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[8] Cooper, R. A., and J. R. Uzmann. 1981. Georges Bank and Submarine Canyon living resources and habitat baselines in oil and gas drilling areas. Northeast Monitoring Program Annual Report for FY 80. Unpubl. manuscr., 34 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

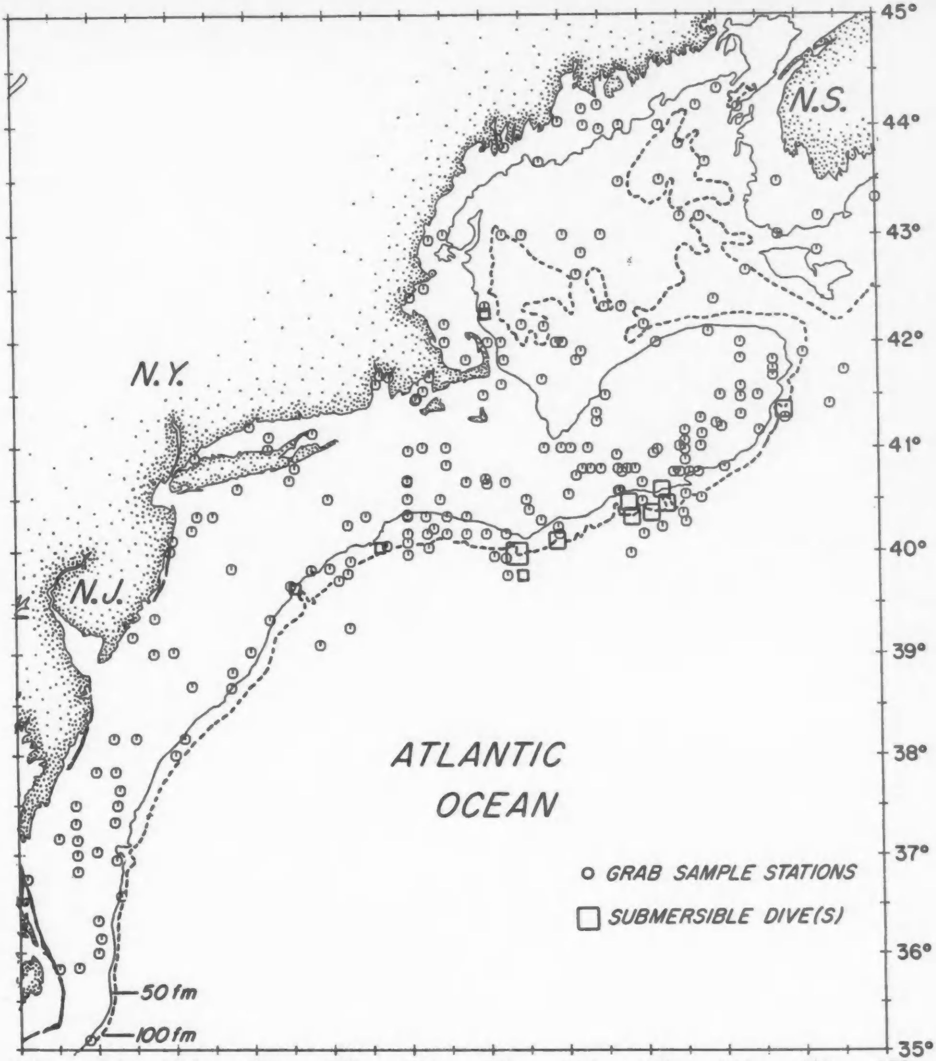

N.Y.
N.J.
N.S.
ATLANTIC OCEAN
○ GRAB SAMPLE STATIONS
☐ SUBMERSIBLE DIVE(S)
50 fm
100 fm
45°
44°
43°
42°
41°
40°
39°
38°
37°
36°
35°
76°
75°
74°
73°
72°
71°
70°
69°
68°
67°
66°
65°

FIGURE 2.—Chart showing the submersible dive(s) sites and grab sample stations containing Ceriantharia. Symbols for submersible dive(s) sites often circumscribe more than one dive, since at this scale some dives were too close together to distinguish with separate symbols (1 fm = 1.83 m).

Relation to Bathymetry

In grab samples, Ceriantharia were found at depths from 6 to 2,329 m, but occurrence was not independent of depth (χ^2, $P < 0.05$). Occurrence was highest from 0 to 100 m, and no Ceriantharia were caught from 501 to 900 m (Fig. 4).

Submersible dive depth range was 80 to 1,930 m (Appendix Tables 1, 2). Cerianthids B, C, and D were seen within the 80-400 m range, no species were

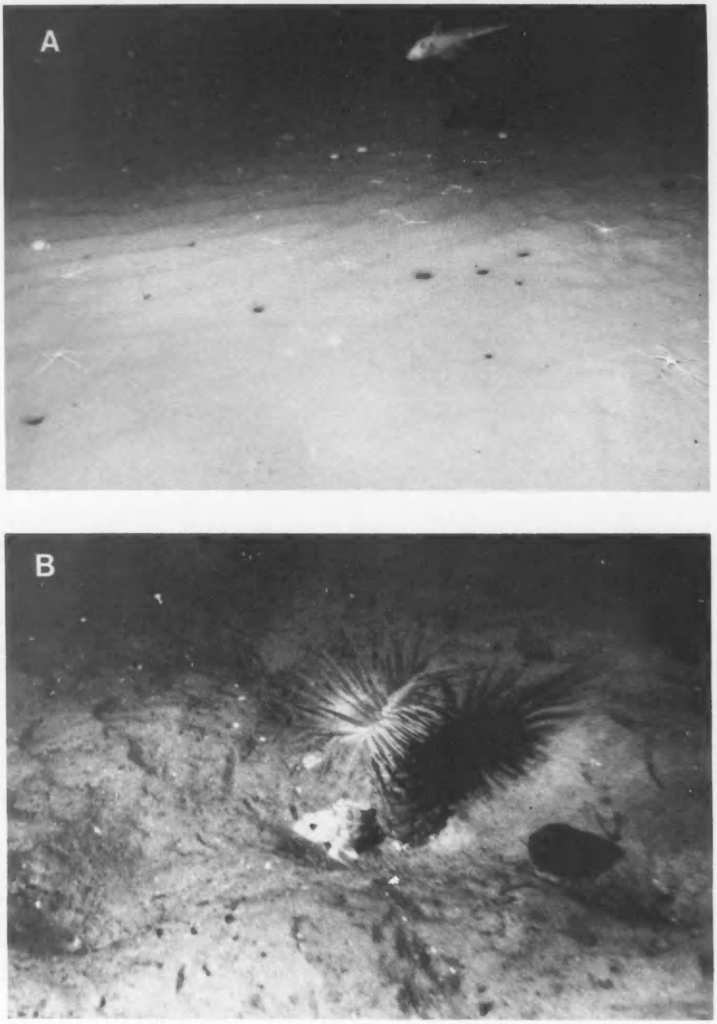
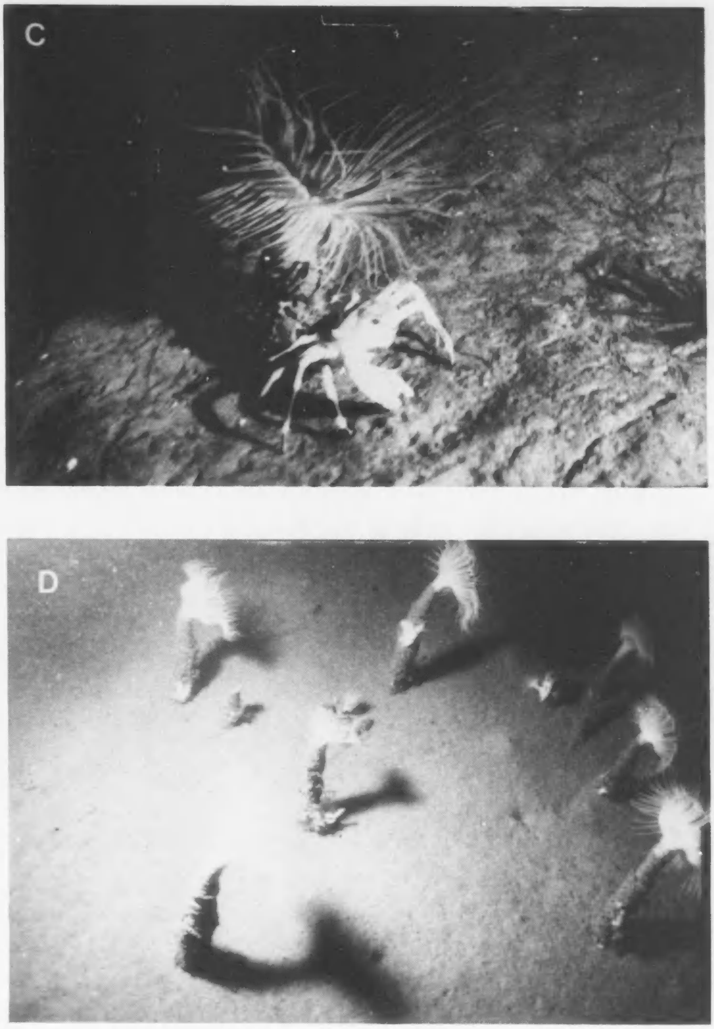


FIGURE 3.—A, B, C, - black and white prints of 35 mm Ektachrome transparencies from a hand-held camera; D - from externally mounted 35 mm brow camera. A. *Alvin* dive 838, axis of Oceanographer Canyon, 1,740 m: Cerianthid A (dark anemones); white brittle stars, *Ophiomusium* sp.; sea urchins, *Echinus affinus*; and a grenadier (Macrouridae) on a calcareous silt-sand substrate. B. *Nekton Gamma* 1974 dive 30, head of Lydonia Canyon, 300 m: Cerianthid B with a blackbelly rosefish, *Helicolenus dac-*



tylopterus, at its tube base, on silt-clay substrate. C. *Nekton Gamma* 1974 dive 30, 300 m: Cerianthid B with a portunid crab, *Bathynectes* sp., at its tube base on silt-clay substrate. D. *Nekton Gamma* 1979 dive 3, head of Block Canyon, 150 m: Cerianthid C with tube epifauna (sponges and colonial white anemones), and redfish, *Sebastes* sp., just visible near center of the photograph on a silt-clay substrate, current direction was from left to right.

TABLE 3.—Morphological features, apparent in photographs taken from submersibles, used to distinguish between four Ceriantharia species seen, and the geographic areas and bathymetric ranges in which they were found (cf. Fig. 3, Appendix Tables 1 and 2).

	Tube height in relation to seafloor		Characteristics of marginal tentacles				
Species	Above	Flush	Length	Arrangement	Coloration	Geographic areas[1]	Depth range (m × 100)
A		X	unequal	multiplanar[2]	dark red, black	6,8	16-19
B	X		unequal	multiplanar	pale purple, pink, tan, or brown	1-8, 10	1-4
C	X		equal	parabolic[2]	white with purple marks	4,9	2-4
D		X	unequal	multiplanar	greenish yellow	10	2-3

[1] 1 - Wilkinson Basin, Gulf of Maine; 2 - Georges Bank; 3 - Corsair Canyon; 4 - Lydonia Canyon; 5 - Gilbert Canyon; 6 - Oceanographer Canyon; 7 - Hydrographer Canyon; 8 - Veatch Canyon; 9 - Block Canyon; 10 - Hudson Canyon.

[2] Used by Meyer (1980) to characterize feeding nets of other passive suspension feeders.

observed at depths from 400 to 1,600 m, and Cerianthid A was seen at depths from 1,600 to 1,930 m (Table 3).

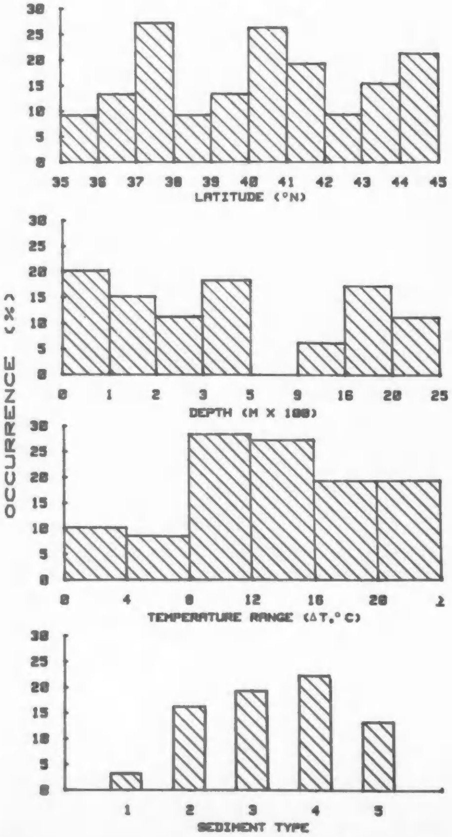


FIGURE 4.—Ceriantharia occurrence (% of grab sample stations) in relation to latitude, depth, temperature range (ΔT = summer high minus winter low), and sediment type. Depth stratum size was determined by pooling, from shallow to deep, adjacent 100 m depth intervals until enough observations were available for a chi-square test. Sediment type codes are 1 - gravel; 2 - gravel/sand, silt, mud or clay; 3 - sand; 4 - silt/sand; 5 - silt/clay.

Relation to Bottom Water Temperature

Temperature observations were sparse for grab sample stations, so, the extreme range of temperature (Δ T), a commonly used measure of climatic variability (MacArthur 1975), was used to compare temperature with Ceriantharia distribution; Δ T equals the difference between extreme annual recorded temperatures (summer high minus winter low), obtained from various published sources, and measurements, made by the NEFC. Site ranges were grouped for plotting: 0° to 3.9°C, 4° to 7.9°C, 8° to 11.9°C, 12° to 15.9°C, 16° to 19.9°C, and >19.9°C. Temperature range changed significantly with latitude and depth. Largest Δ T's generally dominated shelf waters south of lat. 41°N, and inshore waters (Fig. 5).

Ceriantharia occurrence at grab sample stations was not independent of temperature range (χ^2, $P < 0.05$); occurrence was highest on the continental shelf where Δ T was from 8° to 15.9°C (Fig. 4).

All submersible dives were performed in July or August. Bottom water temperatures (external

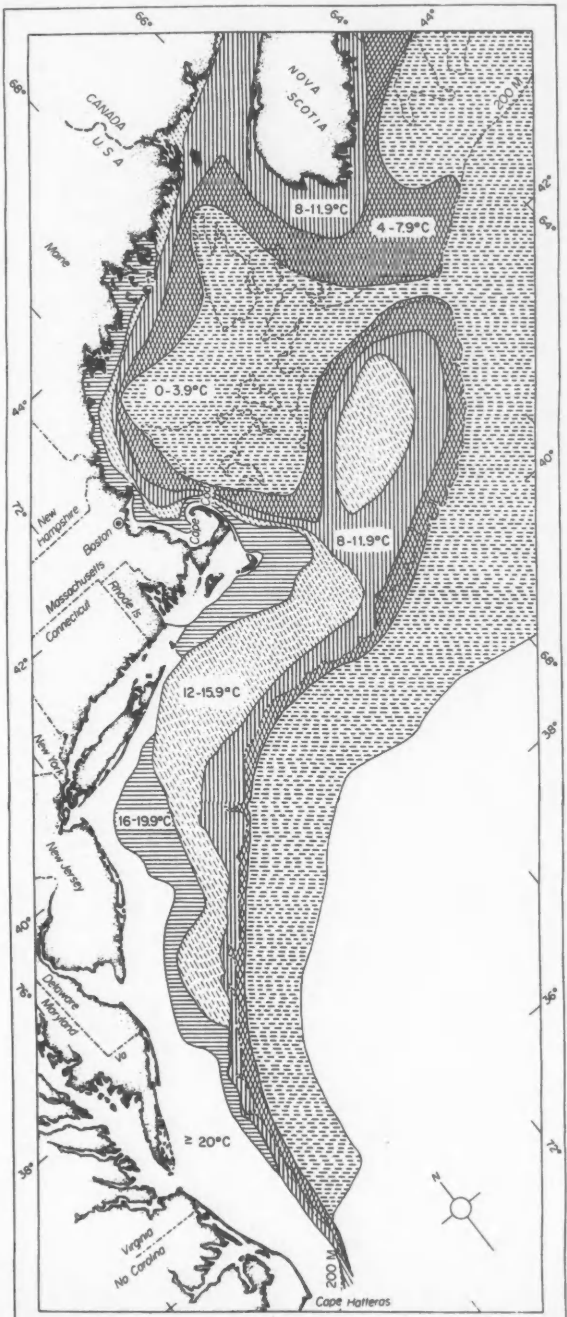

CANADA
U S A
NOVA SCOTIA
Maine
New Hampshire
Boston
Massachusetts
Rhode Is
Connecticut
New York
New Jersey
Delaware
Maryland
Va
Virginia
No Carolina
Cape Hatteras
Cape Cod
200 M
200 M
8-11.9°C
4-7.9°C
0-3.9°C
8-11.9°C
12-15.9°C
16-19.9°C
≥ 20°C
N
66°
64°
44°
42°
40°
38°
36°
68°
72°
76°
74°
70°

FIGURE 5.—Distribution of extreme range in bottom water temperature (summer maximum minus winter minimum) in the Middle Atlantic Bight (from Wigley and Theroux 1981) and New England region (Theroux and Wigley, text footnote 3).

thermometer observations) decreased with depth; temperatures ranged from 5° to 13°C at depths <500 m and declined gradually from 5°C at 500 m to 3.5°C at 1,900 m (Appendix Tables 1, 2). Depth-temperature profiles of three *Alvin* dives (Fig. 6) indicate depths of 500 to 600 m were a transition zone; deeper bottom water temperatures decreased little with depth, in comparison to shallower temperatures. Ceriantharids B, C, and D were seen at temperatures of 5.3° to 13.0°C, and Cerianthid A was observed only in colder, deeper water, in the narrow range of 3.5° to 3.9°C (Appendix Tables 1, 2).

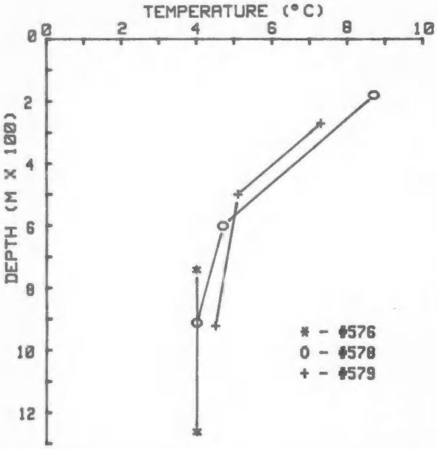


FIGURE 6.—Depth-temperature profiles constructed from observations (of external thermometers) made on the bottom during three *Alvin* dives in Veatch Canyon. Temperature stabilized at about 500-600 m.

Relation to Sediments

Ceriantharia occurrence at grab sample stations was not independent of sediment type (χ^2, $P < 0.05$); they rarely inhabited 100% gravel sediments (Fig. 4). However, when stations with 100% gravel sediments were not included, occurrence was independent of sediment type (χ^2, $P > 0.05$). Although occurrence in silt-clay sediments was lower than in other unconsolidated sediments (Fig. 4), this may be a result of the large proportion of silt-clay sediment stations at depths >500 m, where Ceriantharia were scarcer; if only silt-clay sediments from shallower than 500 m are analyzed, occurrence is more than 20%.

Photographic transect profiles of submersible dives (Appendix Table 2, depths <400 m) provided information on Ceriantharia abundance with respect to substrate, depth, temperature, transect direction, and distance (Figure 7 shows one profile). Based on the number of sightings in various substrata (Appendix Tables 1, 2) and the transect profiles, about 70% of the Ceriantharia inhabited silt-sand and silt-clay sediments. However, they also commonly occurred in rarer gravelly substrates (less than about 50% gravel cover on sand or clay; only about 20% of the total seafloor viewed). They were not seen in coarse sand sediments (usually rippled and/or in dune formations).

The clay substrate observed from submersibles was actually a semiconsolidated mud (Cooper et al. in press); the term clay was used to differentiate it from sand substrates, but clay may only be a minor constituent.

Spatial Pattern

Ceriantharia density and biomass estimates from grab sample data were determined for comparison to other studies (e.g., Sanders 1956; Pearce et al. 1981; Reid et al. 1981; Caracciola and Steimle 1983). However, because no replicate sampling was done at over 90% of the stations, density and biomass were not analyzed further. For stations with anemones or whole tubes, mean density was 35.7 m^{-2} ($N = 168$, 95% C.L. = ± 12.1, range = 1.7 to 1,370 m^{-2}). Mean station biomass (anemone blotted wet weight) was 48.6 g m^{-2} ($N = 139$, 95% C.L. = ± 35.4).

On the quantitative submersible dives, Ceriantharia density ranged from 0 to 0.414 m^{-2} $dive^{-1}$ (Appendix Table 2). The maximum density in one photographic frame was 6.6 m^{-2}. The photographic transect profiles (Fig. 7) showed Ceriantharia populations shallower than 400 m were spatially aggregated. No quantitative information was available for the Cerianthid A populations seen in the axes of Oceanographer and Veatch Canyons.

The largest aggregation encountered (head of Lydonia Canyon, Fig. 7) was over 0.5 km wide and composed mostly of Cerianthid B, with some Cerianthid C individuals. The dives were run over a permanent station marker (37 khz pinger) positioned on a 14-15 m high knoll. Substrate atop the knoll was gravel-sand, near the base and surrounding the knoll was silt-sand. Approximately half of the Ceriantharia aggregation occupied the gravel-sand sediments. Ceriantharia were the dominant megafauna in the area, other common megafauna were galatheid crabs, *Munida iris* Milne-Edwards, and

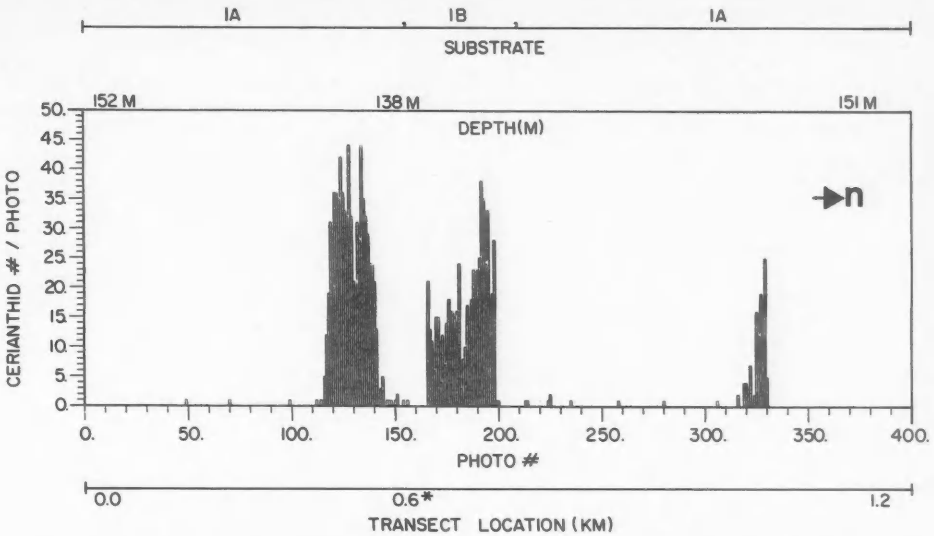


FIGURE 7.—One example, from 1980 *Johnson-Sea-Link* dives 15 and 16 in Lydonia Canyon, of the photograph-by-photograph transect profiles of Ceriantharia abundance constructed for quantitative submersible dives during which Ceriantharia density exceeded 0.1 m^{-2} $dive^{-1}$, at depths of less than 400 m. Substrate codes: 1 - sand base, 1A - silt veneer, 1B - greater than 5% gravel cover. A permanent station marker (37 khz pinger) was located at 0.6 km into the transect, as denoted by the asterisk.

asteroids on gravel-sand, and shell-less hermit crabs, *Catapagurus* sp., on silt-sand. Galatheids were also observed on silt-sand sediments, often near ceriantharian tubes. A qualitative observation made on several submersible dives was that Ceriantharia "forests" (aggregations) were often associated with rises in seafloor topography.

Functional Role

Figure 8 (data from 1979 *Nekton Gamma* dive #3 in Block Canyon) shows Cerianthid C frequency of occurrence and number of associated species (diversity) plotted by photographic frame. The substrate throughout the dive was a low-relief silt-clay, and

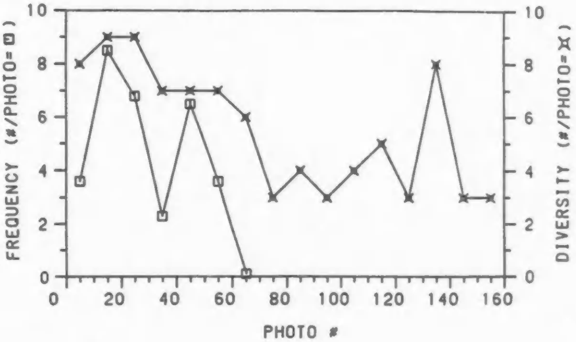


FIGURE 8.—Cerianthid C abundance and diversity (number of species) of associated fauna along a 1.0 km photographic transect from 1979 *Nekton Gamma* dive #3. Each data point represents the sum of 5 adjacent photographic frames: species diversity increased significantly in areas with Ceriantharia (Mann-Whitney test, $P < 0.01$).

the depth and temperature ranges were 137 to 183 m, and 13.0° to 10.7°C. Mean number of species was significantly higher in photographs with Ceriantharia (Mann-Whitney test, $P < 0.01$): Three groups of epifauna (hydroids, sponges, and small white anemones; Fig. 3D) were attached to Ceriantharia tubes only and not found on the surrounding substrate. Also, blackbelly rosefish, *Helicolenus dactylopterus* (De La Roche) (Fig. 3B), and redfish, *Sebastes* sp. (Fig. 3D), abundances were higher in the Cerianthid C patch (0.40/frame and 0.18/frame, respectively) than in the adjacent area (0.03/frame and 0.00/frame); about half of the fish were nestled at tube bases.

At other dive locations, motile megafaunal species often seen nestled near tubes included portunid crabs (*Bathynectes* sp.) (Fig. 3C); jonah crabs, *Cancer* sp.; pandalid shrimps, *Pandalus* sp.; American lobsters, *Homarus americanus* Milne-Edwards; hakes, *Urophycis* spp.; and greeneyes *Chloropthalmus agassizii* Bonaparte.

Two Cerianthid B tubes (50 m apart) and adjacent sediments were collected with the grab sampler of the submersible *Johnson-Sea-Link*, in the head of Oceanographer Canyon at a depth of 293 m. The tubes were separated from the adjacent sediments immediately after the submersible surfaced. The volume of each tube was less than the volume of adjacent sediments (80% fine sand, <0.5 mm; 10% coarse sand; 10% silt) (Appendix Table 3). After preservation and staining, the macrofauna (>0.5 mm) were identified for each sample (Appendix Table 3): Polychaetes were dominant and the three most abundant polychaete species inhabiting the Ceriantharia tubes were absent or scarce in the adjacent sediments; *Polycirrus eximius* (Leily) (a tentacle feeder which sweeps the water and substratum for food), *Marphysa* sp. (a jawed omnivore), and a filter-feeder, *Potamilla neglecta* (Sars) (Fauchald 1977; Fauchald and Jumars 1979).

DISCUSSION

Collection Gear

Gear differences largely account for the differences in Ceriantharia size and density estimates from grab samples versus photographs. Due to limitations in resolution, photographs provide valid data only on larger epifauna (Emery et al. 1965; Barham et al. 1967; Wigley and Emery 1967). However, since the estimated depth of penetration of a 0.1 m^2 Smith-McIntyre grab sampler, the gear used most frequently in this study, is only 3 to 5 cm in unconsolidated substrates (Smith and McIntyre 1954), and large ceriantharian tubes often extend much deeper than 5 cm below the seafloor (Sebens fn. 5), making them difficult to dislodge, if the primary objective is to sample large individuals and document the associations between tubes and other fauna, then photographs and direct observations are more useful than grab samples.

Species Identification

Ceriantheopsis americanus and *Cerianthus borealis*, identified from grab samples, occurred within the geographic and bathymetric ranges noted previously for these species (Table 1). Unfortunately, many Ceriantharia samples were discarded, and none of the available samples from depths greater than 500 m contained anemones for taxonomic identification.

The morphological features used to distinguish between the four species seen from submersibles (Table 3) may not individually be reliable; tentacle coloration may vary noticeably within a species (Arai 1971; Uchida 1979). However, taken together, we feel the features were consistent enough to indicate we saw four species of adult Ceriantharia: *C. borealis* (probably Cerianthid B), two unidentified species (Cerianthids C and D) from depths shallower than about 500 m, and another unidentified species (Cerianthid A) living deeper down the continental slope.

The conclusion that Cerianthid B is *C. borealis* is based on the similarities between our descriptions of Cerianthid B morphology and distribution (Table 3), and information from other studies on *C. borealis* (Table 1; Gosner 1979). The only other previously identified inhabitant of the study area, *C. americanus*, was probably not encountered on our submersible dives; the deepest record found for *C. americanus* was about 70 m (Pearce et al. 1981), whereas our shallowest submersible dive was to a depth of 80 m.

Sebens (in press) described two unidentified Ceriantharia species which occur at depths >1,000 m in the Northwest Atlantic: Unidentified Species II (seen at depths >1,500 m) resembles Cerianthid A (Table 3, Fig. 3A), Cerianthid A in Valentine et al. (1980), and a photograph of unidentified Ceriantharia taken by Grassle et al. (1975) at depths of 1,550 to 1,830 m just south of New England. The distinction Sebens (in press) makes between Unidentified Species I (seen at depths of >1,000 m) and Unidentified Species II (Cerianthid A) is that Species II is smaller (Table 1). Grassle et al. (1975) and

Hecker et al. (1980) also reported seeing small unidentified Ceriantharia at about 1,300 and 1,000 m, respectively. We saw (from submersibles) no Ceriantharia from 1,000 to 1,600 m for comparison.

In addition to the six documented species above, other Ceriantharia sighted in or near the region include two possible species photographed by Hecker[9]: one at depths of 1,800 to 2,800 m (from Lydonia Canyon to Cape Lookout, NC), which resembles a stout black Cerianthid B, and another resembling Cerianthid A (except its tube extends above the seafloor) at depths of 500 to 1,000 m off Cape Hatteras. Rowe and Menzies (1969) photographed Ceriantharia on the continental slope (at depths of 400 to 3,000 m) south of Cape Hatteras (about lat. 34°N) which they guessed to be *Ceriantheomorphe brasiliensis* Carlgren. However, they presented no photographs for comparison and collected no voucher specimens. The *C. brasiliensis* specimens identified by Carlgren (1931) were from Brazil, South America, and its resemblance to other slope species is uncertain. Submersible dive time devoted to in situ documentation and collection of specimens is obviously needed in order to identify the deep-water species[10].

Relation to Latitude

North of Cape Cod and Georges Bank (lat. 42° to 44°N) the continental shelf is dominated by the Gulf of Maine, a feature unlike the rest of the shelf in the region because of its topographic irregularity and because it reaches depths of more than 100 m closer to shore. The lack of tidal mixing below 100 m over much of the gulf, and the fact that the principal source of its bottom water is thermally stable continental slope water introduced through the Northeast Channel, results in water temperature stratification which keeps the gulf bottom water temperatures virtually constant throughout the year (TRIGOM-PARC 1974; Rowe et al. 1975; Ingham et al. 1982, p. 43). The narrow extreme range of bottom water temperature (Δ T) dominant from lat. 42° to 43°N (Fig. 5) may account for low Ceriantharia occurrence at grab sample stations there (Fig. 4), while peaks in occurrence are evident at lat. 40° to 41°N (shelf just south of Cape Cod, including southern Georges Bank), and from 44° to 45°N (shelf off Nova Scotia) may be associated with more favorable intermediate temperature ranges which prevail there (8° to 15.9°C). High Ceriantharia occurrence at grab sample stations between 37° to 38°N is in part due to high occurrence at stations in the lower half of Chesapeake Bay; occurrence was 56% at nine Bay Stations and 23% at 52 shelf/slope stations. However, our data is too sparse and inconclusive to make a bay versus non-bay comparison, or explain the high occurrence at shelf stations in this area.

According to Gosner (1971), the continental margin from Cape Hatteras to Nova Scotia is divided into two faunal provinces with respect to benthic invertebrates: a Boreal (cold-temperate) province north of Cape Cod, and a Virginian (warm-temperate) province of Cape Cod, MA. Theroux (in press) considers the situation to be more complex and to depend on the species considered, but agrees that Cape Cod and Georges Bank are the beginning of a rapid transition from cold to warm temperate fauna, and suggests that the transition is associated with Georges Bank and Nantucket Shoals thermal fronts (Fig. 5; Ingham et al. 1982, p. 40-41).

Using Gosner's (1971) faunal province descriptions, our submersible data indicate that, in addition to *C. americanus*, at least two other warm-temperate species inhabit the northwest Atlantic continental shelf (Cerianthids C and D). The only cold-temperate shelf species, Cerianthid B (probably *C. borealis*) ranges south to Cape Hatteras (Tables 1, 3). The last species we saw (Cerianthid A) is bathyal.

Relation to Bathymetry

Bathymetric zonation of benthic fauna has been previously described for the continental shelf-slope region of the northwest Atlantic (Wigley and Emery 1967; Rowe and Menzies 1969; Sanders and Hessler 1969; Rowe 1972; Grassle et al. 1975; Haedrich et al. 1975, 1980; Hecker et al. 1980; Valentine et al. 1980; Wigley and Theroux 1981). Rowe et al. (1982) cautioned, "'zones' that previous investigations have described apparently are a function both of the animal groups studied and distribution of samples with depth". Thus, our discussion of Ceriantharia zonation is limited to depths <2,000 m, since below that depth there were no submersible data to support the grab sample data.

Ceriantharia distribution, as determined from the grab sample data (Fig. 4), our submersible observations (Table 3), and data from other investigations (Table 1) imply boundaries (defined here as depths characterized by distinct changes in the benthic community's species composition) to Ceriantharia distribution exist at about 500, 900, and 1,600 m.

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[9] B. Hecker, Lamont-Doherty Geological Observatory, Columbia University, Palisades, NY 10964, pers. commun. October 1984.

[10] For all photographed, but unidentified slope species, we know of only one voucher specimen (of Unidentified Species I), presently located at the Harvard Museum of Comparative Zoology, Cambridge, MA.

Our submersible data indicate that shelf species were confined to depths of less than about 400 m, and the bathyal species (Cerianthid A) was seen between 1,600 and 2,000 m. Published reports indicate another unidentified species lives deeper than about 1,000 m (Grassle et al. 1975; Hecker et al. 1980; Sebens in press). Similar depth zonation of slope fauna inhabiting the study area have been reported for isopods (Menzies et al. 1973), demersal fishes (Musick[11]), and megafauna captured in trawls (Haedrich et al. 1980). Some environmental factors, suggested as causes for observed distributions, are temperature, sedimentation rates, and substrate types (summarized by Haedrich et al. 1975, 1980).

The depth interval between about 400 and 600 m on the continental slope south of New England is a temperature transition zone; shallower bottom waters experience larger seasonal temperature variations than stable deeper waters (Sanders and Hessler 1969; Haedrich et al. 1975). Depth-temperature profiles (Fig. 6) made on *Alvin* dives in Veatch Canyon showed larger depth related temperature variations also occurred shallower than 500 to 600 m. The shelf species (Cerianthids B, C, and D) may not be able to tolerate and/or thrive in the cold stable conditions below 500 m.

The Cerianthid A population, we saw deeper than 1,600 m in the axis of Oceanographer Canyon, inhabited sediments high in biogenic carbonates; canyon axes may act as settling basins for suspended matter being funneled downcanyon (Valentine et al. 1980). Rowe and Menzies (1969) attributed increases in suspension-feeder concentration, in photographs from the upper slope (200-800 m) and at the slope base (3,000 m) off North Carolina, to increased detritus accumulation resulting from downslope movement and concentration by the prevailing bottom currents. Haedrich et al. (1980) stated, in reference to the depth zonation of megabenthic fauna on the slope off southern New England, that "zonation must result to some degree from varying strategies that promote success along a food resource gradient".

Haedrich et al. (1975) suggested boundaries to zones of larger epifauna, at about 400 and 1,000 m on the continental slope south of New England, result from physical changes in the slope environment. MacIlvaine (1973, p. 30-70) reported on the physical environment in the same area (sediment type, suspended sediments, and slope gradient). The zone between 400 and 1,000 m consists largely of homogeneous silt-sand substrate, near-bottom suspended sediments at 520 m were 50 to 60 μg/L (about 25% organics), and the slope gradient is about 1.4°. Deeper than about 1,000 m there are more variable sediment features (stiff clayey silt sediments which are smooth or hummocky, talus slopes, and rock outcrops), suspended sediments were 20 μg/L (about 45% organics) at 1,000 m and 80 μg/L (about 80% organics) at 1,670 m, and the slope gradient is steeper (7.6°).

Suspension feeders rely on current velocity and nutrient load for their food supply. Substrate variability deeper than 1,000 m may enhance Ceriantharia occurrence down to 2,000 m: Features such as hummocks may act as perches for suspension feeders, placing them up higher where current is swifter and their food supply is replenished more rapidly (Hughes 1975; Dyer 1980; Sebens 1984). Higher suspended sediments and percentage of organics may further enhance Ceriantharia occurrence below 1,600 m, as compared with 1,000 or 520 m. The lesser slope gradient between 400 and 1,000 m probably results in lower near bottom current velocities; near the shelf-slope break in Oceanographer Canyon, bottom currents are swifter at 105 to 300 m than at 650 m, due primarily to a difference in slope gradient (Valentine in press). Thus, increased slope gradient may enhance Ceriantharia occurrence below 1,000 m.

Other mechanisms may affect ceriantharian depth zonation such as the direct effects of pressure (Siebenallar and Somero 1978), or predators (Paine 1966; Rex 1976); however, data were not available to evaluate these factors.

Submarine canyons received particular attention during submersible dive activities because of the potential entrainment of discharges from oil exploration activities into productive canyon environments (Cooper and Uzmann fn. 8). Bathymetric zonation of slope fauna may be altered and/or species abundance enhanced by submarine canyons (Rowe 1971; Haedrich et al. 1975). The conduitlike nature and substrate heterogeneity of canyons have both been implied as explanations for observed faunal enrichment in canyons as opposed to adjacent noncanyon slope areas (Rowe and Menzies 1969; Rowe 1971, 1972; Haedrich et al. 1975; Hecker et al. 1980; Valentine et al. 1980; Rowe et al. 1982). Although we had no adjacent slope dives to compare with the canyon dives, Ceriantharia were common in canyons and have been suggested to be canyon "indicator" species (Rowe 1972). In the future, we hope a canyon-slope comparison of Ceriantharia species' diversity and abundance will be made.

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[11] Musick, J. A. 1976. Community structure of fishes on the continental slope and rise off the Middle Atlantic Coast of the U.S. Manuscript presented at Joint Oceanographic Assembly, Edinburgh, September. (Copies available from: J. A. Musick, Virginia Institute of Marine Science, Gloucester Point, VA 23062, USA).

Relation to Bottom Water Temperature

Wigley and Theroux (1981) found that total macrofaunal density in the Middle Atlantic Bight generally increased directly with increasing temperature range (Δ T). Ceriantharia occurrence at grab sample stations followed this trend until Δ T reached 15.9°C, after which it decreased (Fig. 4). Why an intermediate temperature range may be favorable to Ceriantharia is unknown. Wide ranges might entail harmful extremes of temperature, while narrower ones may be too constant at an unfavorable level, or larval stages may benefit from some degree of fluctuation for maximal development (Andrewartha and Birch 1954, p. 129-205). Information on how temperature affects ceriantharian metabolism, activity patterns, and development is lacking.

Marine organism distributions are largely controlled by temperature (Hutchins 1947; Crisp 1965; Gosner 1971). The most obvious effect of temperature on invertebrate distributions is exclusion of species from areas with unsuitable thermal regimes (Kinne 1970). Submersible data on ceriantharian geographic and bathymetric distribution demonstrate allopatric speciation which we believe is primarily a response to temperature.

Relation to Sediments

The presence of silt is characteristic of depositional areas which may be favorable to suspension feeders (Rowe and Menzies 1969). Wigley (1968) described Ceriantharia as common inhabitants of silty-sand sediments on Georges Bank. Through resuspension, surficial deposits are potential food for Ceriantharia (Rhoads 1974). In addition to low deposition, substrate instability may account for the scarcity of Ceriantharia in 100% gravel and rippled coarse sand substrate. Shifting substrates, such as the 100% gravel sediments at grab sample stations or the rippled sand dunes observed from submersibles, may harm suspension feeders through clogging of feeding apparatus, or the burial of larvae (Sanders 1956; Ross 1968; Rhoads and Young 1970; Rhoads 1974).

However, Ceriantharia were generally cosmopolitan with respect to substrate (Fig. 4; Appendix Tables 1, 2). They are well adapted to withstand strong currents, sediment movement, and extreme deposition of fine material because their tubes provide firm anchorage (Frey 1970) and protection against clogging or burial (Pearce 1972). Pearce et al. (1976) found Ceriantharia were dominant macrofauna in fine carbon-rich sediments stressful to other benthic species, near New York Bight sewage sludge disposal sites.

Just as 100% gravel substrate is unfavorable for burrowing, a gravel veneer might also be expected to limit space available for burrowing. However, on submersible dives, Ceriantharia were frequently seen in gravel-covered areas (less than about 50% gravel cover). These deposits, probably Pleistocene ice-rafted glacial debris, are exposed in areas which usually experience higher currents than adjacent areas (Valentine et al. 1980; Valentine in press), a favorable consideration for suspension feeders.

Spatial Pattern

Local conditions of food supply, substrate, or microtopography, may enhance Ceriantharia aggregation (Fig. 7). Local differences in food supply may allow Ceriantharia to survive in aggregations. Grassle et al. (1975) observed that strongly clumped suspension-feeders were able to maintain aggregations because their food supply was continually renewed. Unusually high Ceriantharia abundances near a sewage sludge/dredge spoil disposal area may have occurred owing to the increased amounts of organic matter (Pearce et al. 1976).

Grassle et al. (1975) found Ceriantharia, similar to Cerianthid A, more randomly distributed on the continental slope, south of Cape Cod (depth of 1,465 to 1,830 m, homogeneous sandy silt-clay substrate). In comparison, substrata in canyon heads where aggregations were observed from submersibles are heterogeneous (Hecker et al. 1980; Valentine et al. 1980). Our grab samples showed the same contrast between heterogeneous substrata shallower than 500 m and homogeneous silt-sands and clays downslope (Shepard and Theroux fn. 4). Since invertebrates are capable of substrate selectivity (Thorson 1966; Gray 1974), a variable substrate may be characterized by patchy inhabitant distributions (Hecker et al. 1980).

The Cerianthid B aggregation in Lydonia Canyon (Fig. 7), located on a knoll, may benefit from elevated positioning and swifter currents (Hughes 1975; Sebens 1984), thus aggregations may also form in response to local changes in surface elevation.

Functional Role

An increase in structural complexity of the substrate vertically and/or horizontally increases the number of microhabitats, and if the appropriate colonizers and mortality sources are present, within-habitat diversity will likely be increased (Steimle and Stone 1973; Abele 1974; Hughes 1975; Woodin 1976, 1978; Connell 1978; Suchanek 1979; Hulbert et al. 1982). Ceriantharia tubes may increase species diversity and abundance on featureless soft bottom areas by 1) attracting motile megafauna seeking refuge near tubes and 2) serving as a favorable substrate for epifauna and infauna, particularly suspension-feeders and tubiculous species.

By acting as a three-dimensional refuge, the tubes may ease predation pressure on smaller motile species (Ware 1972; Whoriskey 1983). Demersal fish and crustaceans similar to those we observed have been noted by others in association with Ceriantharia (Uzmann et al. 1977; Hecker et al. 1980; Valentine et al. 1980). The species most commonly observed near tubes, *Helicolenus dactylopterus*, *Sebastes* sp., and *Bathynectes* sp., characteristically exhibit thigmotactic behavior.

Associations similar to the ones we found between suspension feeders and Ceriantharia tubes in Block Canyon (Figs. 3D, 8), and polychaetes and tubes from Oceanographer Canyon (Appendix Table 3), have been recorded for Ceriantharia and polychaetes (Kingsley 1904; O'Connor et al. 1977), phoronids (Ponder 1971; Emig et al. 1972; Hartog 1977), and bivalves (Ponder 1971). These associations have been alternately referred to as commensalism or inquilinism; we prefer the latter definition as it highlights the role of the ceriantharian tube. Emig et al. (1972) speculated that *Cerianthus maua* Carlgren tentacles may act as baffles, causing waterborne food particles to settle out, and become available to suspension feeders (*Phoronis australis* Haswell) inhabiting the *C. maua* tubes, in which case the term commensalism may be more appropriate. However, Emig et al. also stated that increased food supply is probably a secondary benefit to the phoronids and that the suitability of the tube as a settlement surface for larvae motivates the association. O'Connor et al. (1977) studied a *Pachycerianthus multiplicatus* Carlgren population inhabiting deposit substrates (85% silt-clay, 15% sand) off Ireland and suggested tubes were prime settlement surface for the larvae of inquiline filter-feeding polychaetes, *Myxicola infundibulum* (Renier). The associates (sponges, hydroids, and colonial anemones) of Ceriantharia tubes in Block Canyon are generally nonmotile so they probably had to arrive on the tubes as larvae. More unstable substrate surrounding the tubes may be less suitable as a settlement surface for larvae of suspension feeders (Rhoads and Young 1970, 1971; Rhoads 1974).

The vertical aspect of Ceriantharia tubes may enhance diversity and abundance by 1) allowing vertical stratification of trophic types (MacArthur and Levins 1964; Hughes 1975; Schoener 1975; Ausich and Bottjer 1982), and 2) affording inhabitants, such as the filter feeder *Potamilla neglecta*, elevated feeding stations where clogging by resuspended sediments is less likely, and current velocities tend to be greater (Dyer 1980), thus the food supply is more rapidly renewed (Hughes 1975; Sebens 1984).

The stable nature of the tubes may serve species behaviorally inclined to attach themselves to firm substrate. The three species of polychaetes, *Polycirrus eximius*, *Marphysa* sp., and *Potamilla neglecta*, most abundant on ceriantharian tubes caught in Oceanographer Canyon, but rarely found in the adjacent sediments (Appendix Table 3), usually attach their tubes to solid surfaces such as stones, algae, or hydroids (Gosner 1971; Fauchald and Jumars 1979).

Infaunal species may also gain relief from predation pressure by inhabiting ceriantharian tubes. The feltlike tubes are generally more consolidated that the sediments surrounding them, thus more difficult to graze. Ponder (1971) viewed protection as the principal benefit to a leptonid bivalve, *Montacutona ceriantha* Ponder, inquiline with *Cerianthus* sp. in Japanese waters. Protection may be enhanced for tubiculous infauna since their retraction may be stimulated by a similar response to disturbance by the host ceriantharian (Emig et al. 1972).

Ceriantharia tubes may serve as a preferential food source for some infauna. O'Connor et al. (1977) noted sipunculids, *Golfingia elongata* (Keferstein), inquiline with *Pachycerianthus multiplicatus* had tube remains in their guts. Scavengers, such as *Marphysa sanguinea* may benefit from the inquilinism for this reason.

Ceriantharia may also negatively affect the infauna in sediments adjacent to the tubes; large motile species, attracted to the tubes for shelter, might selectively graze near tubes. We hope to investigate Ceriantharia "forest" communities more thoroughly on future submersible cruises: Substrate collections taken away from tubes will further define their functional role. We believe Ceriantharia influence the ecology of the northwest Atlantic continental shelf and slope more than has been revealed from data collected by conventional surface techniques alone; methods inadequate for collecting deep-burrowing adults, and providing information on behavioral and spatial relationships between Ceriantharia and other community residents.

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APPENDIX TABLE 1.—Summary of statistics for submersible dives during which only qualitative
= gravel sand; 1c = shell-sand; 2 = rocky cover; 2a = cobbles; 2b = boulders; 2/1 or 3 = rocks
and temperatures listed are those in which Ceriantharia were seen, for dives without Ceriantha
species: 0 = absent; A, B, C, or D = species recorded on video tapes; + = Ceriantharia s

Year/submersible dive(s)[1]	Geographic name	Lat. N	Long. W	Horizontal distance travelled (km)
1971 PC8 9/26 (1,2)	Wilkinson Basin	42°17′	69°58′	1.8
1973 NG 4	Veatch Canyon	40°00′	69°38′	1.8
7	Veatch Canyon	39°59′	69°37′	2.0
11	Veatch Canyon	39°57′	69°33′	2.0
12	Veatch Canyon	39°56′	69°33′	2.0
13	Veatch Canyon	39°55′	69°33′	2.0
14	Veatch Canyon	40°00′	69°37′	2.0
1974 NG 1, 2, 4-6	Veatch Canyon	40°00′	69°37′	1.0 km^2
9	Hydrographer Canyon	40°12′	69°05′	1.3
10	Hydrographer Canyon	40°08′	69°02′	1.2
12	Hydrographer Canyon	40°09′	69°06′	0.7
13	Hydrographer Canyon	40°04′	69°05′	1.3
14	Oceanographer Canyon	40°30′	68°10′	3.0
15	Oceanographer Canyon	40°28′	68°10′	3.0
16	Oceanographer Canyon	40°29′	68°15′	1.7
17	Oceanographer Canyon	40°29′	68°09′	2.2
18	Oceanographer Canyon	40°27′	68°07′	1.5
19	Oceanographer Canyon	40°23′	68°08′	2.0
20	Oceanographer Canyon	40°20′	68°05′	2.6
23	Corsair Canyon	41°21′	66°11′	3.0
24	Corsair Canyon	41°24′	66°14′	4.0
25	Corsair Canyon	41°23′	66°10′	1.0
26	Corsair Canyon	41°20′	66°06′	3.2
27	Lydonia Canyon	40°32′	67°42′	1.5
28	Lydonia Canyon	40°32′	67°44′	2.2
29	Lydonia Canyon	40°31′	67°40′	1.7
30	Lydonia Canyon	40°28′	67°41′	1.4
31	Lydonia Canyon	40°23′	67°41′	2.1
32	Lydonia Canyon	40°24′	67°38′	1.3
33	Gilbert Canyon	40°22′	67°49′	2.0
34	Gilbert Canyon	40°22′	67°55′	2.4
35	Oceanographer Canyon	40°20′	68°12′	2.1
36	Veatch Canyon	39°59′	69°39′	1.8
37	Veatch Canyon	39°59′	69°38′	1.8
38	Veatch Canyon	39°59′	69°37′	1.8
1976 AL 667	Veatch Canyon	39°59′	69°35′	3.3
668	Veatch Canyon	39°51′	69°33′	?
669	Veatch Canyon	39°47′	69°32′	?
670	Veatch Canyon	39°52′	69°34′	?
671	Veatch Canyon	39°58′	69°37′	3.2
672	Veatch Canyon	40°01′	69°37′	7.4

litative data were collected. Substrate definitions: 1 = sand base; 1a = silt-sand; 1b = rocks on sand or clay base; 3 = clay base; 3a = silt-clay; 3b = gravel-clay. Substrates riantharia all substrates and temperatures recorded on the dive are listed. Ceriantharia haria seen but species not identified.

ntal ce led)	Dive depth range (m × 100)	Ceriantharia depth range (m × 100)	Temp (°C)	Substrate	Cerianthid species
	1.2-2.2	1.2-1.6	6.1	1a,1b,3a	B
	1.5	1.5	11.1	1a,3a	+
	1.9-3.0	2.4-3.0	7.2-9.2	3a	+
	1.6	1.6	9.4-10.0	1a	+
	1.7	1.7	10.6	1a	+
	2.5	2.5	7.2-7.8	1a,1c	+
	1.8	—	8.3-9.2	1a,3a	0
m^2	1.7-2.6	2.1	8.3-11.1	1a	+
	1.5-2.5	1.6-2.4	8.9-10.8	1a	+
	2.0-3.0	2.8-3.0	9.2-11.1	1a	+
	1.5-2.7	1.6-1.7	8.3-11.1	1a,2/1	+
	1.9-2.1	1.9-2.1	10.8-11.1	1a	+
	1.7-2.4	?	?	1a,2a/1,3a	+
	1.3-2.7	1.3-2.7	9.4-11.0	1a,1c,3a	B
	1.6-2.2	1.6	9.7-11.9	1a,2a/1	+
	1.7	1.7	11.1	3a,3b	B
	1.9-3.0	2.7	8.2-9.7	1a	B
	1.9-3.0	2.4	9.7-10.4	3a	B
	1.9-3.0	2.1-2.9	8.1-12.8	1a	B
	1.5-3.0	1.8-3.0	6.4-9.7	1a,2a/3,3a,3b	B
	1.1-2.4	1.5	9.4	1b,2a/1	B
	2.2-3.0	2.4-2.7	5.8-9.2	1b	B
	1.5-3.0	2.6-2.9	6.9-7.2	1a,1b	B
	1.5-3.0	1.6-3.0	7.2-11.4	1a,1c	B
	1.4-3.0	1.4-2.7	8.3-10.8	1a,1c	B
	1.4-2.9	2.4-2.7	8.9	1a	B
	1.7-3.0	2.6-2.9	8.6-10.8	3a,3b	+
	1.5-2.9	1.5-2.7	7.5-12.8	1a,1b,1c	B
	1.8-2.2	—	9.2-9.7	1a	0
	2.0-3.0	2.1-2.7	9.2-10.8	1a	B
	1.5-3.0	2.4-2.6	9.4-12.2	1a	B
	1.8-3.0	1.8	7.2-12.2	1a	B
	1.6-2.3	—	10.0-14.1	1a,2/3,3a	0
	1.8	—	11.4	1a	0
	1.7-2.5	2.5	7.8-10.6	3a	+
	1.3-6.7	1.4-4.0	?	3a	+
	9.1-14.4	—	4.0	3a	0
	14.0-19.3	18.4-19.3	3.5	3a	A
	8.0-15.1	—	4.0	3a	0
	1.9-6.8	2.9	10.5	3a	+
	1.4-2.2	1.6-2.2	9.0	3a	B

APPENDIX TABLE 1.—*Continued.*

Year/submersible dive(s)[1]	Geographic name	Lat. N	Long. W	Horizontal distance travelled (km)
1978 AL 835	Oceanographer Canyon	40°24′	68°10′	3.3
836	Oceanographer Canyon	40°17′	68°07′	0.7
837	Oceanographer Canyon	40°28′	68°10′	3.1
838	Oceanographer Canyon	40°12′	68°05′	6.1
839	Oceanographer Canyon	40°26′	68°07′	3.1
840	Oceanographer Canyon	40°21′	68°09′	0.4

[1] Submersible abbreviations: PCB = *Perry Model C8*, NG = *Nekton Gamma*, AL = *Alvin*.

APPENDIX TABLE 2.—Summary of statistics for submersible dives during which quantitative d
Gamma (3.6 m^2 $photo^{-1}$); JSL = *Johnson-Sea-Link* (7 m^2 $photo^{-1}$). Substrate definitions: 1
2a = cobbles; 2b = boulders; 2/1 or 3 = rocks on sand or clay base; 3 = clay base; 3a =
Ceriantharia were seen, for dives without Ceriantharia all substrates and temperatures reco
(cf. Table 3). Densities are mean # m^{-2}; * = Ceriantharia present but less than 0.01 m

Year/submersible dive(s)		Geographic name	Lat. N	Long. W	Areal coverage (m^2)	Dive depth range (m × 100)
1975 AL	576	Veatch Canyon	39°54′	69°36′	4,170	7.4-12.6
	577	Veatch Canyon	39°59′	69°35′	6,840	2.1-4.6
	578	Veatch Canyon	39°56′	69°35′	5,355	1.8-9.1
	579	Veatch Canyon	39°55′	69°37′	5,010	2.7-9.2
1979 NG	1	Oceanographer Canyon	40°29′	68°11′	572	1.6-2.3
	2	Oceanographer Canyon	40°28′	68°08′	418	1.7-1.8
	3,4	Block Canyon	40°02′	71°20′	756	1.4-2.4
	12	Hudson Canyon	39°30′	71°22′	868	1.5-3.0
	14	Hudson Canyon	39°38′	71°25′	378	1.6-3.0
1980 AL	1034	Oceanographer Canyon	40°29′	68°10′	11,070	2.1-3.9
	1035	Oceanographer Canyon	40°18′	68°07′	8,580	7.3-13.2
	1036	Oceanographer Canyon	40°25′	68°09′	10,005	2.1-6.2
1980 JSL	3,4	Georges Bank	40°43′	67°28′	5,992	0.9
	7,8	Georges Bank	40°37′	67°45′	6,230	0.8
	12,14	Lydonia Canyon	40°28′	67°42′	3,759	1.5-3.0
	15,16	Lydonia Canyon	40°32′	67°43′	5,138	1.2-1.9
1981 JSL	2	Georges Bank	40°43′	67°28′	2,765	0.9
	3,4,5	Georges Bank	40°37′	67°45′	5,110	0.8
	8,9	Lydonia Canyon	40°32′	67°43′	5,551	1.2-1.7
	12,13	Lydonia Canyon	40°28′	67°42′	4,655	1.4-2.6
	16	Oceanographer Canyon	40°30′	68°09′	3,150	1.4-1.5
	19,20	Oceanographer Canyon	40°26′	68°09′	5,593	2.0-4.6

izontal tance velled km)	Dive depth range (m × 100)	Ceriantharia depth range (m × 100)	Temp (°C)	Substrate	Cerian-thid species
3	1.5-7.0	1.5-3.0	7.1-10.8	1a,1b,3a	+
7	10.0-12.9	—	?	3a	0
1	1.3-3.5	1.3-2.9	?	3a	+
1	14.5-18.7	16-18.7	3.7-3.9	1a	A
1	1.4-5.2	1.4-3.0	7.8-10.7	1a,1b,2a/3,3b	+
4	9.0-9.5	—	?	3a	0

tative data were collected. Vessel information: AL = *Alvin* (15 m^2 photo^{-1}); NG = *Nekton* ions: 1 = sand base; 1a = silt-sand; 1b = gravel-sand; 1c = shell-sand; 2 = rocky cover; e; 3a = silt-clay; 3b = gravel-clay. Substrates and temperatures listed are those in which s recorded on the dive are listed. Cerianthid species: 0 = absent, A, B, C, or D = species 01 m^{-2}).

depth nge 100)	Ceriantharia depth range (m × 100)	Temp (°C)	Substrate	Ceriantharia Species	Density (# m^{-2}	±	95% C.L.)
-12.6	—	4.0	3a	—	0		—
-4.6	2.7-4.0	5.3-7.6	3a	B	*		—
-9.1	2.0-3.6	5.5-9.2	3a	B	0.025	±	0.012
-9.2	2.7-3.8	5.5-7.3	3a	B	0.037	±	0.013
-2.3	1.6-2.0	11.0	1a,1b,2b/1	B	0.086	±	0.039
-1.8	1.7-1.8	—	3b	B	*		—
-2.4	1.4-1.8	9.1-13.0	3a	C	0.414	±	0.124
-3.0	1.5-2.9	—	3a	—	0		—
-3.0	3.0	—	3a	B,D	*		—
-3.9	2.7-3.4	9.4	1a,3a,2a/3	B	0.016	±	0.008
-13.2	—	5.8	3a	—	0		—
-6.2	3.1	9.8-11.2	3a	B	*		—
	0.9	9.6	1a	B	*		—
	0.8	9.2-9.5	1a	B	*		—
-3.0	1.7-2.9	10.3-11.9	3a,1a	B,C	0.102	±	0.034
-1.9	1.2-1.9	11.6-11.9	1a,1b	B,C	0.357	±	0.077
	0.9	8.3	1a	B	*		—
	0.8	8.1	1a	B	*		—
-1.7	1.3-1.6	9.9-10.8	1a,1b	B,C	0.377	±	0.062
-2.6	1.7-2.5	9.6-9.9	3a,1a	B,C	0.030	±	0.012
-1.5	1.4-1.5	9.9-10.3	3a,1a,1c	B	0.029	±	0.008
-4.6	2.1-3.4	9.4-10.4	3a,3b,1a	B	*		—

APPENDIX TABLE 3.—Macrofauna (>0.5 mm) inhabiting two Cerianthid B tubes,
sampler (290 cm^2, 5-10 cm penetration depth) from the *Johnson-Sea-Link*'s mani
yon. A tube and the adjacent sediments were collected together, put in the same
sible was aboard ship.

Tube (200 cc)	No.	Sediments (800 cc)	No.	Tube
		Sample #1		
Annelida		Annelida		Annelida
Oligochaeta	2	Oligochaeta	7	Polycha
Polychaeta		Polychaeta		*Polyc*
Polycirrus eximius	14	*Prionospio cirrifera*	11	*Marpl*
Marphysa sp.	8	*Aricidea catherinae*	7	*Potan*
Potamilla neglecta	6	*Goniada maculata*	3	*Podar*
Prionospio cirrifera	5	*Exogones hebes*	2	*Exogo*
Ninoe gayheadi	2	*E. verugera*	2	*E. he*
Aricidea catherinae	1	*Ninoe gayheadi*	2	*Aricio*
A. cerrutii	1	*Ophalina accuminata*	2	Tereb
Exogone hebes	1	*Aglaophamus igalis*	1	*Thary*
E. verugera	1	*Ampharete arctica*	1	*Typos*
Glycera capitata	1	*Cirratulus cirratus*	1	Arthropod
Lumbrinereis sp.	1	*Micronephtys minuta*	1	Crustac
Schistomerengos		*Neopodarke*		*Photi*
caeca	1	*woodsholea*	1	Cope
Tharyx annulosus	1	*Nereis zonata*	1	Crab
Arthropoda		*Polycirrus eximius*	1	
Crustacea		*Prionospio cirrifera*	1	
Tanaidacea	38	*Protodorvillea*		
Photis dentata	2	*gaspeensis*	1	
Caprella linearis	1	*Typosyllis* sp.	1	
Janira alta	1	Arthropoda		
Total	87	Crustacea		
		Copepoda	6	
		Tanaidacea	3	
		Hyperiidea	1	
		Total	56	

tubes, and adjacent sediments (silt-sand), collected by a grab s manipulator arm, at a depth of 293 m in Oceanographer Can- same sample container, and separated as soon as the submer-

Tube (1200 cc)	No.	Sediments (1,600 cc)	No.
		Sample #2	
nelida		Annelida	
olychaeta		Oligochaeta	15
Polycirrus eximius	25	Polychaeta	
Marphysa sp.	16	*Aricidea catherinae*	49
Potamilla neglecta	11	*Prionospio cirrifera*	28
Podarke obscura	9	*P.* juv.	14
Exogone verugera	5	*Tharyx annulosus*	13
E. hebes	3	*Goniada maculata*	10
Aricidea catherinae	1	*Ophalina accuminata*	7
Terebellidae	1		
Tharyx acutus	1	*Prionospio steenstrupi*	5
Typosyllis alternata	1	*Dodecaceria* sp.	3
hropoda		*Exogone hebes*	3
rustacea		*E. verugera*	3
Photis dentata	4	Nephtyidae juv.	3
Copepoda	1	*Paraonis gracilis*	3
Crab zoea	1	*Anobothorus gracilis*	2
Total	79		
		Schistomerengos sp.	2
		Tharyx acutus	2
		T. sp.	2
		Aglaophamus circinata	1
		Drilonereis longa	1
		Eunice pennata	1
		Haploscoloplos sp.	1
		Lumbrinereis fragilis	1
		Neopodarke woodsholea	1
		Nereis zonata	1
		Protodorvillea gaspeensis	1
		Spio sp.	1
		Anthropoda	
		Crustacea	
		Diastylis sp.	1
		Janira alta	1
		Pagurus annulipes	1
		Total	176

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CARTILAGE AND BONE DEVELOPMENT IN SCOMBROID FISHES

Thomas Potthoff, Sharon Kelley, and Joaquin C. Javech[1]

ABSTRACT

Early development of cartilage and bone was examined in representative species of the scombroid fish families Scombrolabracidae, Gempylidae, Trichiuridae, Scombridae, Istiophoridae, and Xiphiidae from cleared and stained larval size series. Development of the dorsal and anal fins and their pterygiophore supports, development of the neural and haemal spines and hypural complex, and ossification of the vertebrae were studied. The first appearance and location of these skeletal elements in cartilage were noted, and then the direction of new additions was observed. Direction of ossification of these elements was also noted. There were three major kinds of verebral column development: The first was shared by Scombrolabracidae, Scombridae in part - Scombrini, Scomberomorini, and Thunnini; the second was shared by Gempylidae, *Sarda* (Scombridae in part - Sardini), Istiophoridae, and Xiphiidae; the third kind was found in *Trichiurus* (Trichiuridae). Saddle-shaped ossifications of the vertebrae were found only in the Scombrolabracidae, and Gempylidae, and Scombridae. Four major kinds of fin and pterygiophore development were observed in the scombroid families: Scombrolabracidae and Scombridae in part - Scombrini shared one kind; Gempylidae, Trichiuridae, and Scombridae in part - Scomberomorini, Sardini, and Thunnini shared another kind, which had some variations for different taxa; Istiophoridae had the third kind; and Xiphiidae had the fourth kind. Initial ossification of the vertebral column started in one place in *Scombrolabrax*, Gempylidae, *Trichiurus*, and *Xiphias*, in two places in *Scomberomorus*, *Sarda*, *Thunnus*, and *Istiophorus*, and in four places in *Scomber* and *Acanthocybium*. From our investigation, we are just beginning to learn about developmental characters and we cannot interpret their full meaning until more developmental work has been accomplished; we can only state that billfish (Istiophoridae, Xiphiidae) are very different from all other scombroids studied and that *Scombrolabrax* shows affinity with the scombroids.

In this paper we describe development of selected osteological features of families in the suborder Scombroidei. We believe that this ontogenetic data will be useful in future taxonomic studies to aid in establishing familial relationships. Under current classification the scombroids comprise various numbers of families. Greenwood et al. (1966) recognized six families in the suborder Scombroidei: Scombridae, Gempylidae, Trichiuridae, Istiophoridae, Xiphiidae, and Luvaridae. Gosline (1968), Potthoff et al. (1980), and Collette et al. (1984) included the family Scombrolabracidae in the Scombroidei, but Johnson (in press) removed it recently. Collette et al. (1984), Leis and Richards (1984), and Tyler et al.[2] removed the Luvaridae from the Scombroidei. For this study we examined ontogenetic series of representative genera of the families Scombrolabracidae, Gempylidae, Trichiuridae, Scombridae (four tribes), Istiophoridae, and Xiphiidae.

Research on the larvae and young stages of scombroids, particularly tunas (Richards and Klawe 1972) has been extensive. In general, most papers deal with the external description of the larvae and juveniles (Okiyama and Ueyanagi 1978); few exist that address the internal morphology and development of scombroids and those are mostly on scombrids. Kramer (1960) described bone development in the mackerel (*Pneumatophorus diego = Scomber japonicus*). Potthoff and Richards (1970), Matsumoto et al. (1972), and Richards and Potthoff (1974) published osteological characters for juvenile scombrids. Cartilage and bone development were described in *Thunnus atlanticus* (Potthoff 1975), *Scombrolabrax heterolepis* (Potthoff et al. 1980), and *Xiphias gladius* (Potthoff and Kelley 1982). Kohno et al. (1984) described fin and cartilaginous fin support development in *Scomber japonicus*. To our knowledge no developmental studies of cartilage and bone have been made for the scombroid families Istiophoridae and Gempylidae, although a part of the research presented here was published in Collette et al. (1984). Since Collette et al. (1984), we have conducted additional research and have discovered several errors in our published observations. We have added developmental series of *Scomber*

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[1] Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

[2] Tyler, J. C., G. D. Johnson, I. Nakamura, and B. B. Collette. Osteology and relationships of the oceanic fish *Luvarus imperialis* (Luvaridae): an acanthuroid not a scombroid. Unpubl. manuscr. National Museum of Natural History, Wash., DC 20560.

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spp., *Scomberomorus* spp., *Acanthocybium solanderi* and *Sarda sarda* (Scombridae), *Trichiurus lepturus* (Trichiuridae), and *Makaira nigricans* (Istiophoridae). We examined numerous juvenile and adult Trichiuridae; our findings are incorporated here. In table 161 of Collette et al. (1984), observations from the gempylid *Diplospinus multistriatus* were erroneously listed under Trichiuridae. In this paper we have revised and corrected that table and incorporated all our new findings (Tables 1, 2).

TABLE 1.—Developmental and osteological features and counts

			Trichiruidae		Scombridae
	Scombrolabracidae (*Scombrolabrax*)	Gempylidae	without tail and pelvic fin, *Trichiurus*	with tail and pelvic fin, *Benthodesmus* *Evoxymetapon* *Lepidopus*	Scombrini (*Scomber*)
Predorsal bones:					
present or absent	absent	present or or absent[2]	absent	absent	absent
number	0	0 or 1	0	0	0
First anteriormost dorsal pterygiophore:					
supports number of fin spines	2	2	2	2	2
inserts in interneural space number	3	2	2	2	3
First anteriormost anal pterygiophore:					
supports number of spines or rays	3	[3]2 or 3	2	[4]3	2
Middle radials:					
present or absent	present	present[5]	present	present	present
Dorsal and anal stay:					
present or absent	present	present	not determined	present	present
ossifies to one or two parts	one part	one or two parts[6]	—	one part	one part
posteriorly bifurcated or nonbifurcated	nonbifurcated	bifurcated	—	nonbifurcated	bifurcated
Pelvic fin:					
spine, ray count	I,5	I,5;I,4;I,2; I,1;I	—	I,1;I,2	I,5
Preural centrum 3:					
neural spine with or without cartilage tip	with	with	—	with	with
haemal spine autogenous or nonautogenous	autogenous	autogenous	—	ontogenetically fused	autogenous
Vertebrae inclusive of urostyle supporting caudal rays:					
number	3	3	—	3	3
Number of vertebrae:					
precaudal + caudal = total	13 + 17 = 30	usually more precaudal, fewer caudal, total 31-67	40 + 126 = 166	fewer precaudal, more caudal, total 99-192	13,14 + 17,18 = 31
Epurals:					
number	3	[7]3	—	1 (ontogenetic fusion from 2)	2
Anterior epural fused with neural arch of Pu_2	No	No	—	No	No

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[1] Data from Fritzsche and Johnson (1980) and G. D. Johnson (text footnote).

[2] *Ruvettus*, *Thyrsitops* and *Tongaichthys* have one predorsal bone.

[3] *Rexea* and *Thyrsites* (*Leionura*) have two spines, *Nealotus* ontogenetically has three spines but second spine fuses to basipterygium during development.

[4] Two of these spines are extreme vestiges.

METHODS

Scombroid larvae were cleared and stained for cartilage and bone (Potthoff 1984) and subsequently measured in millimeters with a calibrated ocular micrometer under a binocular microscope. Notochord length (NL) was measured on preflexion and flexion stage larvae from the anterior tip of the upper jaw to the posterior tip of the notochord. Standard length (SL) was measured from the anterior

for the scombroid families and *Morone*, a primitive perciform fish.

Scombridae—*Continued*						
Scomberomorini (*Scomberomorus*)	Scomberomorini (*Acanthocybium*)	Sardini (*Sarda*)	Thunnini (*Thunnus*)	Istiophoridae (*Istiophorus*)	Xiphiidae (*Xiphias*)	Percichthyidae (*Morone*)[1]
absent 0	absent 0	absent 0	absent 0	absent 0	absent 0	present 3
2	2	2	2	3	1 to 3, mostly 2	3
3	3	2	3	1	2	3
3	not known	3	3	2	1 to 3, mostly 2	3
present	present	present	present	present	absent	present
present one part	present one part	present one part	present one part	present one part	present one part	present one part
nonbifurcated	slightly bifurcated	bifurcated	bifurcated	bifurcated, sometimes non-bifurcated	non-bifurcated	nonbifurcated
I,5	I,5	I,5	I,5	I,2	0	I,5
with autogenous	with autogenous	with autogenous	with autogenous	with autogenous	without non-autogenous	with autogenous
4,5	5	5	4	3	2	3
(16-22) + (24-32) = (41-53)	(30-32) + (31-33) = (62-64)	26 + 25 = 51	fewer precaudal, more caudal, total 39-41	12 + 12 = 24 11 + 13 = 24	15 + 11 = 26 16 + 10 = 26	12 + 13 = 25 11 + 14 = 25
2	2	2	2	3	3	3
No	No	No	Yes	No	No	No

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[5] *Neoepinnula* lacks middle radials.

[6] *Lepidocybium*, *Rexea*, *Diplospinus*, *Paradiplospinus*, *Tongaichthys*, and *Gempylus* have a one-part stay, all other gempylids have a two-part stay.

[7] *Diplospinus* ontogenetically usually has three epurals, posterior two epurals are fused to one in adults, but some *Diplospinus* develop only two epurals.

TABLE 1.—*Continued.*

			Trichiuridae		Scombridae
	Scombrolabracidae (*Scombrolabrax*)	Gempylidae	without tail and pelvic fin, *Trichiurus*	with tail and pelvic fin, *Benthodesmus* *Evoxymetapon* *Lepidopus*	Scombrini (*Scomber*)
Uroneural:					
number	2	2	—	1	1
Hypural 5:					
present or absent	present	present	—	absent	present
fused or separate	separate	separate	—	not known	fused to uroneural proximally
Ontogenetic hypural fusion:					
fusion of hypurals 1 & 2 to ventral plate is in cartilaginous or ossified state	no fusion	if present, ossified	—	not known	cartilaginous
fusion of hypurals 3 & 4 to dorsal plate is in cartilaginous or ossified state	no fusion	If present, ossified	—	not known	cartilaginous or ossified
Procurrent spur (Johnson 1975):					
present or absent	present	present, reduced or absent	—	absent	absent
Stay on 4th pharyngobranchial (G. D. Johnson, text footnote):					
present or absent	absent	absent	absent	absent	present

TABLE 2.—Developmental features for the scombroid

	Neural and haemal arches and spines, parapophyses and hypural parts initially develop in the following places on the notochord by the following sequence. Addition is in a given direction.	Developing pterygiophores and fin spines and rays are added in a direction.
Scombrolabracidae (*Scombrolabrax*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly. 4. Dorsad at center, posteriorly and anteriorly.	First dorsal: anteriorly and posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Gempylidae (*Gempylus*, *Nesiarchus*, *Diplospinus*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly.	First dorsal: posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Trichiuridae (*Trichiurus*)	1. Anterodorsad, posteriorly. 2. Ventrad at center, posteriorly and anteriorly.	Entire dorsal and anal: posteriorly.

Scombridae—*Continued*						
Scomberomorini (*Scomberomorus*)	Scomberomorini (*Acanthocybium*)	Sardini (*Sarda*)	Thunnini (*Thunnus*)	Istiophoridae (*Istiophorus*)	Xiphiidae (*Xiphias*)	Percichthyidae (*Morone*)[1]
1	1	1	1	1	1	2
present separate	present fused to uroneural proximally	present separate	present separate	absent —	present separate	present separate
cartilaginous	cartilaginous	cartilaginous	cartilaginous	cartilaginous or ossified	ossified	no fusion
cartilaginous	cartilaginous or ossified	cartilaginous or ossified	cartilaginous	cartilaginous or ossified	ossifed	no fusion
absent	absent	absent	absent	absent	absent	present
present	present	present	present	present	present	absent

families and *Morone*, a primitive perciform fish.

Sequence of fin and associated pterygiophore development.	First anteriormost dorsal and anal pterygiophore develop from one or two pieces of cartilage.	Number of initial places of ossification along vertebral column; centra develop from saddle-shaped ossifications at bases of neural and haemal arches.
1. Second dorsal and anal concurrently. 2. First dorsal. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	1;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	1;Yes
1. All dorsal rays and pterygiophores dorsoanterior to anal fin. 2. All dorsal rays and pterygiophores opposite future anterior portion of anal fin. 3. All anal rays and pterygiophores.	Dorsal and anal from one piece.	1;No

TABLE 2.—*Continued.*

	Neural and haemal arches and spines, parapophyses and hypural parts initially develop in the following places on the notochord by the following sequence. Addition is in a given direction.	Developing pterygiophores and fin spines and rays are added in a direction.
Scombridae, Scombrini (*Scomber*)	1. Posteroventrad, posteriorly and anteriorly. 2. Ventrad at center, posteriorly and anteriorly. 3. Dorsad at center, posteriorly and anteriorly. 4. Anterodorsad, posteriorly.	First dorsal: pterygiophores anteriorly and posteriorly. Spines: one anteriorly, rest posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Scomberomorini (*Scomberomorus*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly. 4. Dorsad at center, posteriorly and anteriorly.	First dorsal: posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Scomberomorini (*Acanthocybium*)	Not entirely known. Smallest specimen available had already two centers of initial development: anterodorsad and posteroventrad.	First dorsal: probably posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Sardini (*Sarda*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly.	First dorsal: pterygiophores posteriorly. Spines: first one anteriorly, rest posteriorly. Second dorsal: probably anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Thunnini (*Thunnus*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly. 4. Dorsad at center, posteriorly and anteriorly.	First dorsal: pterygiophores posteriorly. Spines: first one anteriorly, rest posteriorly. Second dorsal: anteriorly and posteriorly. Anal: some anteriorly, most posteriorly.
Istiophoridae (*Istiophorus*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, haemal spines posteriorly, parapophyses anteriorly.	Entire dorsal: very few anteriorly, most posteriorly. Anal: very few anteriorly, most posteriorly.
Xiphiidae (*Xiphias*)	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteriorly and anteriorly.	Entire dorsal: anteriorly and posteriorly. Anal: very few anteriorly, most posteriorly.
Percichthyidae (*Morone*)[1]	Anterodorsad, posteriorly. Ventrad at center, posteriorly and anteriorly. Posteroventrad, posteriorly and anteriorly. Initial sequence not known, not known if neural arches and spines develop initially at center.	First dorsal: anteriorly and posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.

[1] Data from Fritzsche and Johnson (1980) and G. D. Johnson (text footnote 3).

Sequence of fin and associated pterygiophore development.	First anteriormost dorsal and anal pterygiophore develop from one or two pieces of cartilage.	Number of initial places of ossification along vertebral column; centra develop from saddle-shaped ossifications at bases of neural and haemal arches.
1. Second dorsal and anal concurrently. 2. First dorsal.	Dorsal and anal from one piece.	4;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	2;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal probably from one piece, anal not known.	4;Not known
1. First dorsal. 2. Second dorsal and anal concurrently. Not known if first dorsal is separated from second dorsal during part of development.	Dorsal from one piece, anal probably from two pieces.	2?;Yes
1. First dorsal. 2. Second dorsal and anal almost concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	2;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal *not* separated from second dorsal during development.	Dorsal from one piece, anal from two pieces.	2;No
1. Second dorsal and anal concurrently. 2. First dorsal. First dorsal and first anal *not* separated from second dorsal and second anal during development.	Variable, dorsal and anal may develop from one or two pieces.	1;No
1. Second dorsal and anal concurrently. 2. First dorsal. Separation or continuity of first and second dorsals not known.	Dorsal and anal from two pieces.	?;No

tip of the upper jaw to the posterior margin of the hypural bones. *Xiphias* larvae were measured from the anterior margin of the eye to the posterior tip of the notochord for eye notochord length (ENL) or from the anterior margin of the eye to the posterior margin of the hypural bones for eye standard length (ESL).

FAMILY SCOMBROLABRACIDAE

Figure 1

Thirty *Scombrolabrax heterolepis* larvae (2.9-10.4 mm NL or SL) were available.

Development of the vertebral column initially started in four places on the notochord: 1) anterodorsad (neural arches and spines of future centra 1-3), 2) posteroventrad (parhypural, hypurals), 3) ventrad at the center (haemal arches and spines on future centra 16-21), and 4) dorsad at the center (neural arches and spines on future centra 12-28). The anterior neural spines were added in a posterior direction whereas the neural and haemal spines at the center of the body were added anteriorly and posteriorly. The two areas of neural spine development coalesced around the eighth neural spine anteriorly and just anterior to the hypural complex posteriorly. The hypurals were added in a posterior direction, but the parhypural and the two autogenous haemal spines were added anteriorly (Table 2). Ossification of the vertebral column in *Scombrolabrax* initially started in one place with the anteriormost neural arches and spines and proceeded in a posterior direction. The hypural complex was the last along the vertebral column to start ossifying. Vertebrae first ossified by forming saddles of bone dorsad and ventrad around the notochord. As ossification proceeded the saddles merged laterally forming an hourglass-shaped vertebra in the lateral view.

Cartilaginous second dorsal and anal fin pterygiophores developed first simultaneously above interneural spaces 15-17 and below interhaemal spaces 16-19 before the anterior neural arches and spines had coalesced. The addition of cartilaginous second dorsal and anal fin pterygiophores was in an anterior and posterior direction. First dorsal fin pterygiophores appeared second above interneural spaces 4-7, to which pterygiophores were added anteriorly and posteriorly, terminating anteriorly in the third interneural space and joining with the second dorsal fin pterygiophores posteriorly. Dorsal and anal fin rays and spines developed in the same sequence as their corresponding pterygiophores, but a little later (Table 2).

Scombrolabrax heterolepis does not develop predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three spines (two supernumerary spines). The posteriormost five or six dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double ray and had a nonbifurcated stay (Table 1).

In *S. heterolepis*, first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the anterior development of the neural spines and the central appearance of haemal spines. The hypural complex development was described by Potthoff et al. (1980). *Scombrolabrax heterolepis* had the basic perciform caudal skeleton (Gosline 1968), with no hypural fusion observed in adults. The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. A procurrent spur was present on the posteriormost ventral secondary caudal ray with a basally foreshortened ray anterior to it (Johnson 1975) (Table 1).

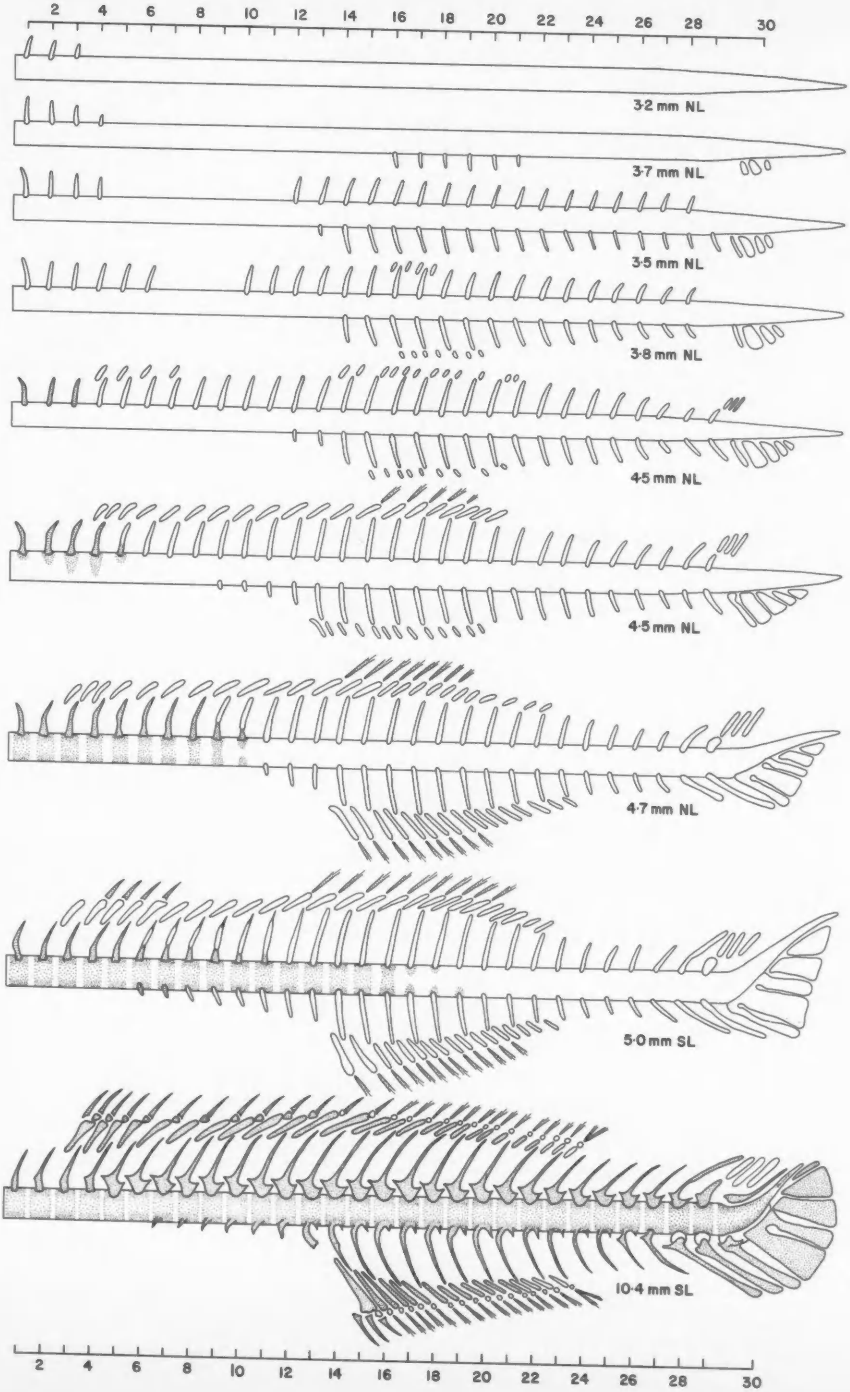
FAMILY GEMPYLIDAE

Figures 2-4

One hundred and ten gempylids in 11 genera were available: 33 *Gempylus serpens* (3.7-9.9, 160 mm NL or SL), 23 *Nesiarchus nasutus*, (2.6-10.2, 55, 242 mm NL or SL), 7 *Neoepinnula orientalis* (3.3-7.1, 112 mm NL or SL), 11 *Nealotus tripes* (3.4-11.9, 24-140 mm NL or SL), 5 *Lepidocybium flavobrunneum* (5.5-35.3 mm NL or SL), 5 *Promethichthys prometheus* (26.4-161 mm SL), 2 *Rexea* sp. (132, 155 mm SL), 2 *Ruvettus pretiosus* (209, 212 mm SL), 1 *Thyrsitops lepidopoides* (160 mm SL), 16 *Diplospinus multistriatus* (3.4-13.5 mm NL or SL), 5 *Thyrsites atun* (= *Leionura*, 83-254 mm SL). Of these, *G. serpens*, *D. multistriatus*, and *N. nasutus* yielded complete developmental series.

Development of the vertebral column initially started in three places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1-6); 2) posteroventrad (hypurals); and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were

FIGURE 1.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scombrolabrax heterolepis*, Scombrolabracidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.


2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
3·2 mm NL
3·7 mm NL
3·5 mm NL
3·8 mm NL
4·5 mm NL
4·5 mm NL
4·7 mm NL
5·0 mm SL
10·4 mm SL
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30

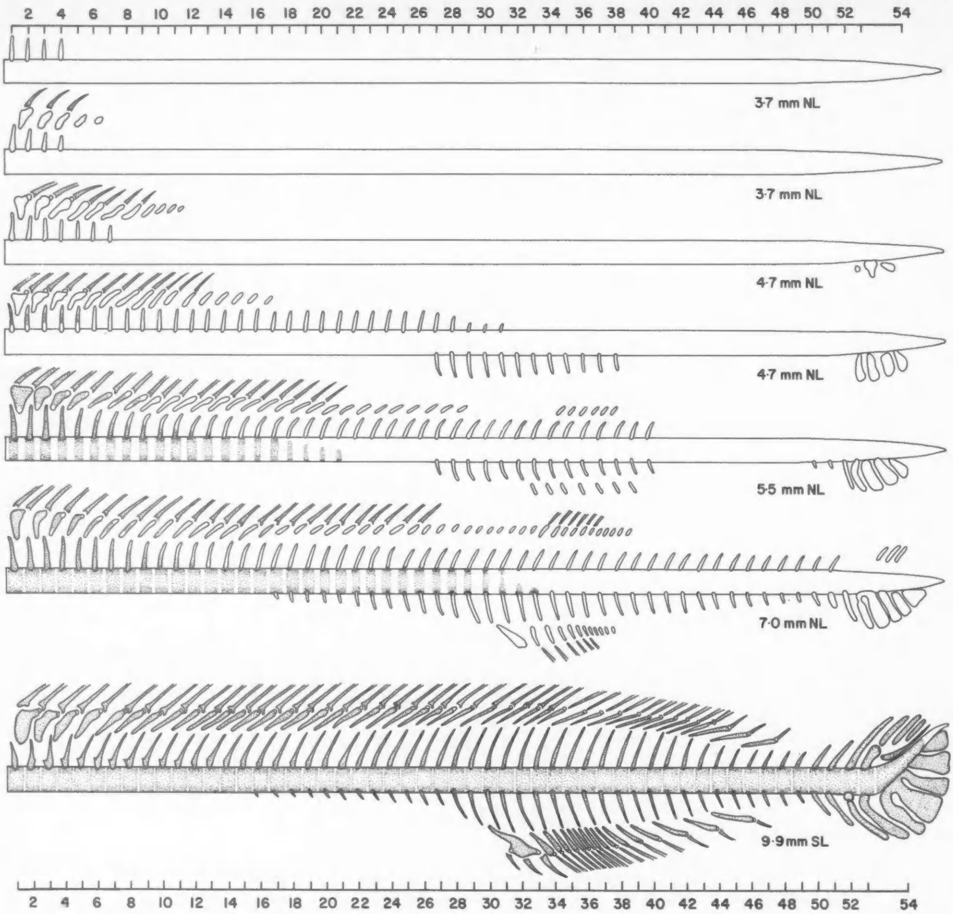


FIGURE 2.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Gempylus serpens*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

added in a posterior direction. Haemal arches and spines developed only when the neural spines reached the caudal area, and they were added in a posterior direction. Parapophyses were added anteriorly. The hypurals were added posteriorly, the parhypural and the autogenous haemal spines were added anteriorly (Table 2). Ossification of the vertebral column in the gempylid genera examined by us initially started in one place and was similar to the ossification in *Scombrolabrax*, except in *Diplospinus* the vertebral column was ossified to preural centrum 6 when the urostyle and the hypurals initially started to ossify. Saddle-shaped vertebral ossifications were observed in all gempylids examined, similar to those described for *Scombrolabrax*.

Gempylids developed first dorsal fin pterygiophores and fin spines first, after only a few cartilaginous neural spines had developed. Development of first dorsal fin pterygiophores and spines was in a posterior direction. During early development the neural spines were anterior to the first dordal fin pterygiophores and fin spines, but later they developed faster and were posterior to the pterygiophores. Pterygiophores of the second dorsal and anal fins developed before the developing first dorsal fin pterygiophores and had joined with the second dor-

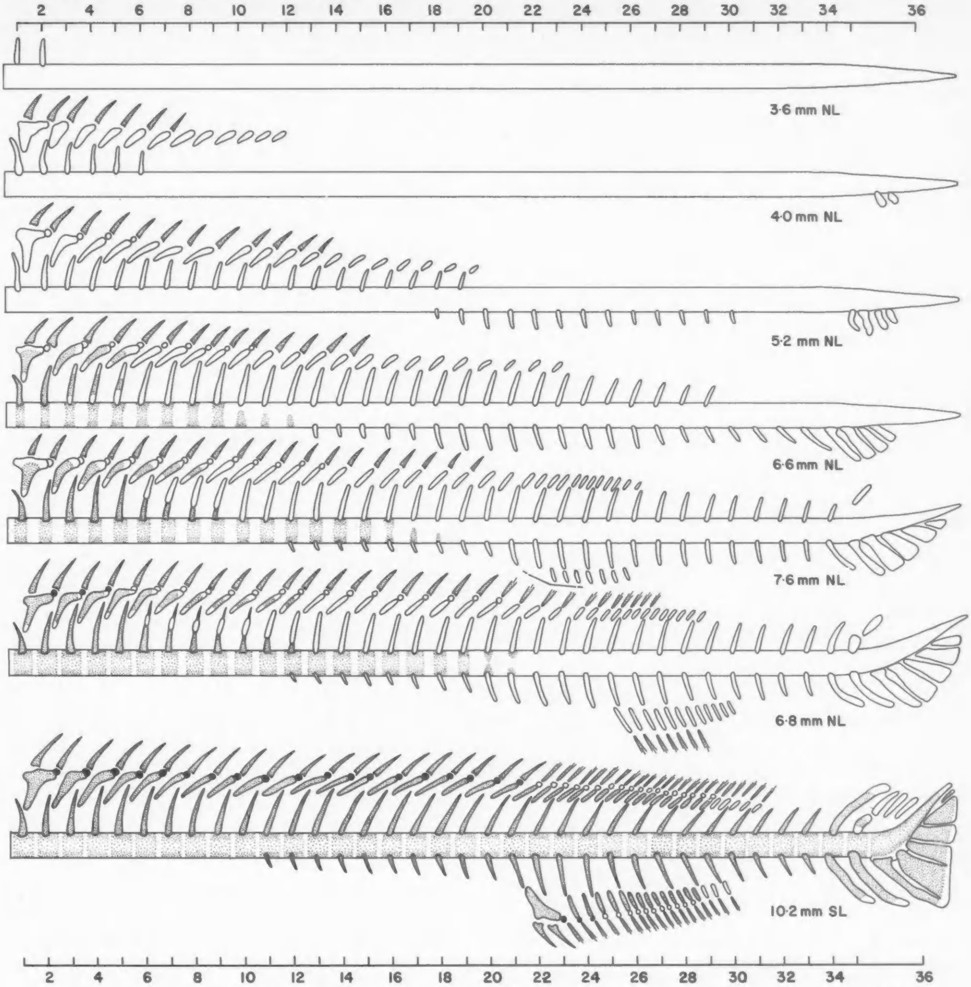
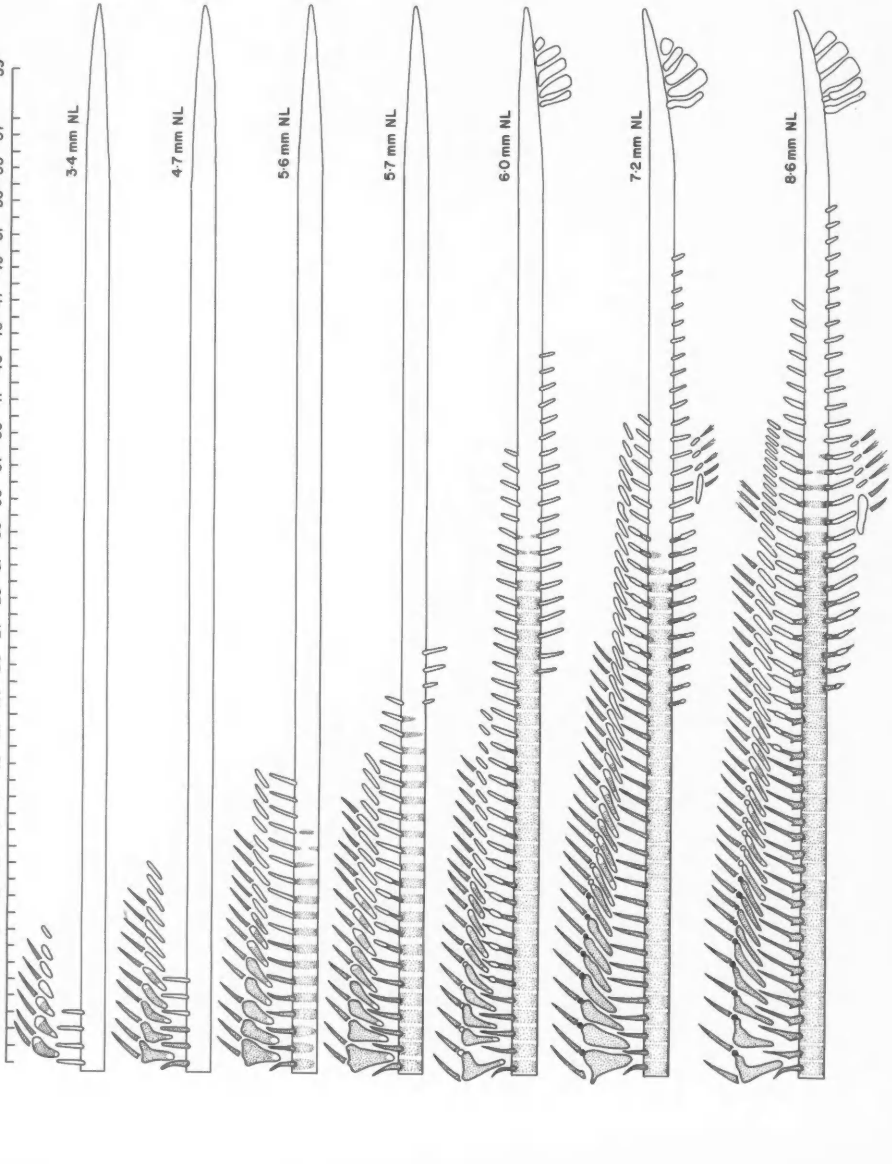


FIGURE 3.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Nesiarchus nasutus*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

sal fin pterygiophores. Addition of second dorsal and anal pterygiophores was then in an anterior and posterior direction. The same development was observed for the second dorsal and anal fin rays and anal spines at slightly greater size (Table 2).

Most gempylid genera lack predorsal bones, except *Tongaichthys* (Nakamura and Fujii 1983), *Ruvettus* (Potthoff's pers. obs.), and *Thyrsitops* (Sato 1983) which have one predorsal bone. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the second interneural space supporting two fin spines (one supernumerary spine). In three Atlantic *Lepidocybium*, the first dorsal pterygiophore inserted in the second interneural space, but in two Pacific specimens it was found in the third space. The first anal pterygiophore was considerably larger than the following pterygiophores and presumably developed from two pieces of cartilage. It supported three anal spines (two supernumerary spines) except in adults of *Rexea*,


3·4 mm NL
4·7 mm NL
5·6 mm NL
5·7 mm NL
6·0 mm NL
7·2 mm NL
8·6 mm NL

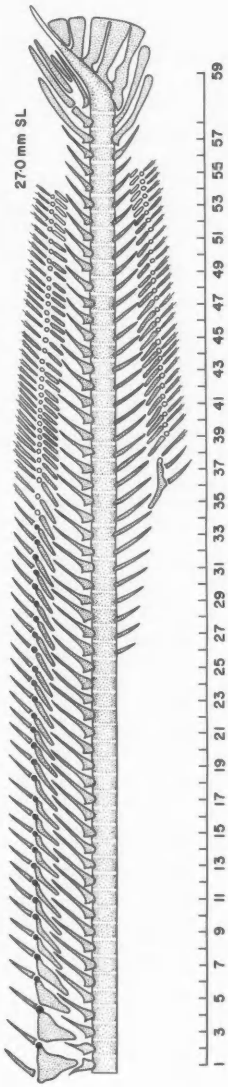


FIGURE 4.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Diplospinus multistriatus*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

Thyrsites (*Leionura*), and *Nealotus* where only two spines were supported (one supernumerary). Larvae of *Nealotus* have three spines associated with the first anal pterygiophore, but in juveniles the second anal spine was fusing to the posterior process of the pterygiophore. No evidence of a similar fusion was observed in *Rexea* or *Thyrsites* (*Leionura*). Gempylids had middle radials in one to six posteriormost dorsal and anal pterygiophores (except *Neoepinnula* lacked middle radials). A double ray, and a two-part posteriorly bifurcated stay was associated with the last dorsal and anal pterygiophore in approximately one half of the genera. *Lepidocybium*, *Gempylus*, *Diplospinus*, *Paradiplospinus*, *Tongaichthys*, and *Rexea* had a one-part posteriorly bifurcated stay (Table 1).

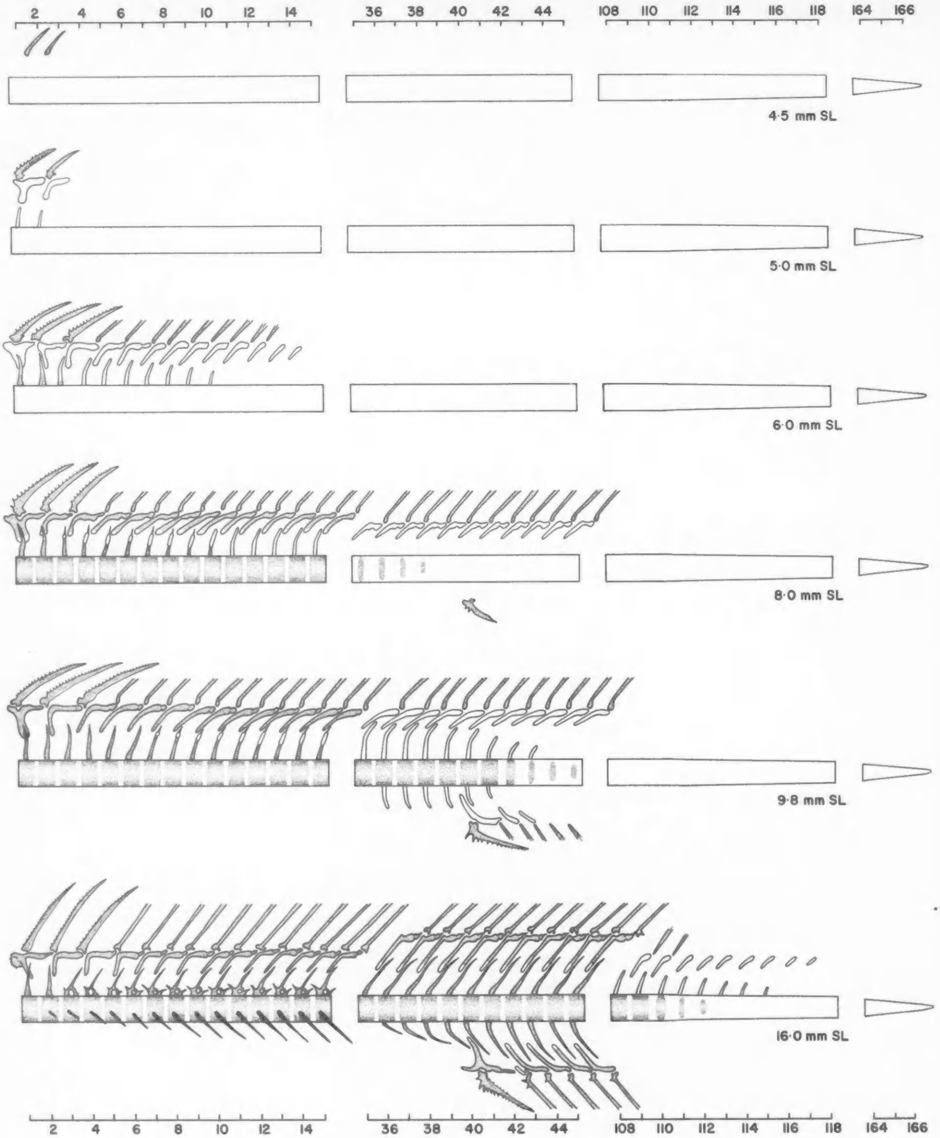
First caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with anterior development of a few neural spines and some first dorsal fin pterygiophores and fin spines. The gempylid genera studied by us developed all parts found in basic perciform caudal skeletons (Gosline 1968), even the smaller second uroneural. Caudal parts then fuse differently in the various genera of adults (Matsubara and Iwai 1958). The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. In the gempylids the procurrent spur on the posteriormost ventral secondary caudal ray may be present, reduced, or absent. Johnson (1975) examined two species in which it was absent (Table 1).

FAMILY TRICHIURIDAE

Figures 5-8

Seventy-three trichiurids in four genera were available: 61 *Trichiurus* (4.5-26, 300, 303, 510 mm TL), 8 *Benthodesmus* (4.5, 12 mm NL, 65-120, 541, 545 mm SL), 3 *Evoxymetapon* (210-550 mm SL), 1 *Lepidopus* (280 mm SL). Only *Trichiurus* yielded a complete developmental series.

Development of the vertebral column in *Trichiurus* initially started in two places on the notochord: 1) anterodorsad (neural arch and spine on future centrum 1), and 2) ventrad at the center (anterior haemal arches and posterior parapophyses). Cartilaginous neural arches and spines were added in a posterior direction. Haemal arches and spines developed when the neural spines reached the anterior future caudal vertebrae. Addition of haemal arches and spines was also in a posterior direction (Table 2). *Trichiurus* lacked a caudal complex. Ossification of the vertebral column started initially in one place, with the anteriormost neural spines and


2
4
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36
38
40
42
44
108
110
112
114
116
118
164
166
4·5 mm SL
5·0 mm SL
6·0 mm SL
8·0 mm SL
9·8 mm SL
16·0 mm SL

FIGURE 5.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Trichiurus lepturus*, Trichiuridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

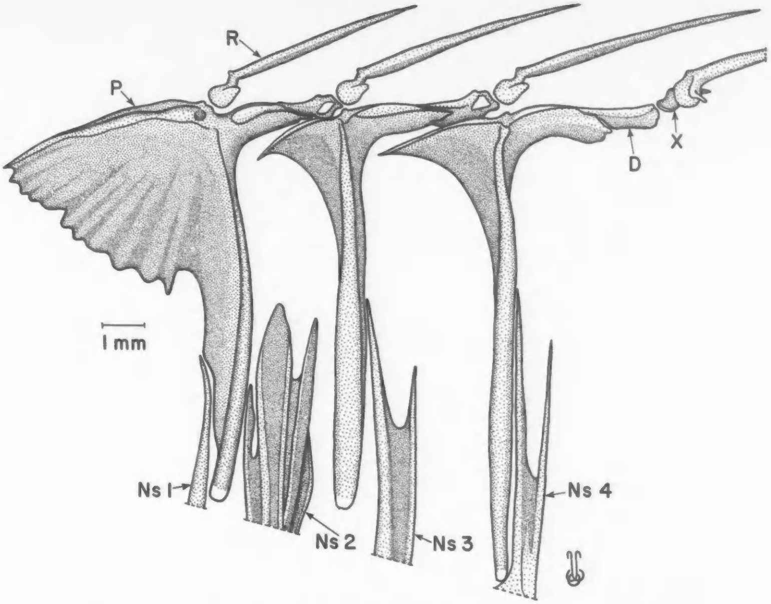

FIGURE 6.—Left lateral view of the anteriormost three dorsal pterygiophores inserting in the interneural spaces 2-4 from a juvenile *Trichiurus lepturus* 510 mm TL. D, distal radial; Ns, neural spine; P, proximal radial; R, ray or spine; X, a new pterygiophore element of unknown homology. Cartilage, white; bone, stippled.

arches and proceeded in a posterior direction. Saddle-shaped ossifications of the vertebrae as seen in Scombrolabrocidae, Gempylidae, and Scombridae were not observed in *Trichiurus*, instead vertebral ossification started laterally on both sides of the notochord as a thin strip of bone. During further development the lateral strip elongated dorsad and ventrad joining the strip from the opposite side and forming a ring of bone around the notochord.

Trichiurus first developed two of the three anterior dorsal fin spines. Next the first dorsal pterygiophore developed. Then dorsal pterygiophores, the third dorsal fin spine, and the dorsal fin rays were added in a posterior direction, with the pterygiophore development being slightly posterior to the ray development and considerably posterior to the neural arch and spine development. The single large anal spine developed first after dorsal fin ray and pterygiophore development had dorsally passed the anterior portion of the anal fin fold. Next, the large first anal fin pterygiophore and some haemal arches and spines developed. Further development consisted of the addition of anal fin rays, pterygiophores, and haemal arches and spines in a posterior direction. The haemal arches and spines and the anal fin rays developed slightly anterior to the anal pterygiophores. The anal pterygiophores were slightly anterior to the dorsal fin ray and pterygiophore development (Table 2).

Trichiurus lacked predorsal bones. The first dorsal pterygiophore supported two fin spines (one supernumerary) and originated from one piece of cartilage. In larvae the first dorsal pterygiophore inserted between the split neural arch and spine of the first centrum, thus inserting into the first and second interneural spaces. However, in adults the first dorsal pterygiophore inserted into the second interneural space. All following interneural and interhaemal spaces accommodated one pterygiophore per space. The first anal pterygiophore was larger than the following pterygiophores, but it developed from one piece of cartilage and supported one supernumerary spine and one ray (Table 1).

The pterygiophores in *Trichiurus* and probably in most if not all species of the Trichiuridae are anatomically different from those of other scom-

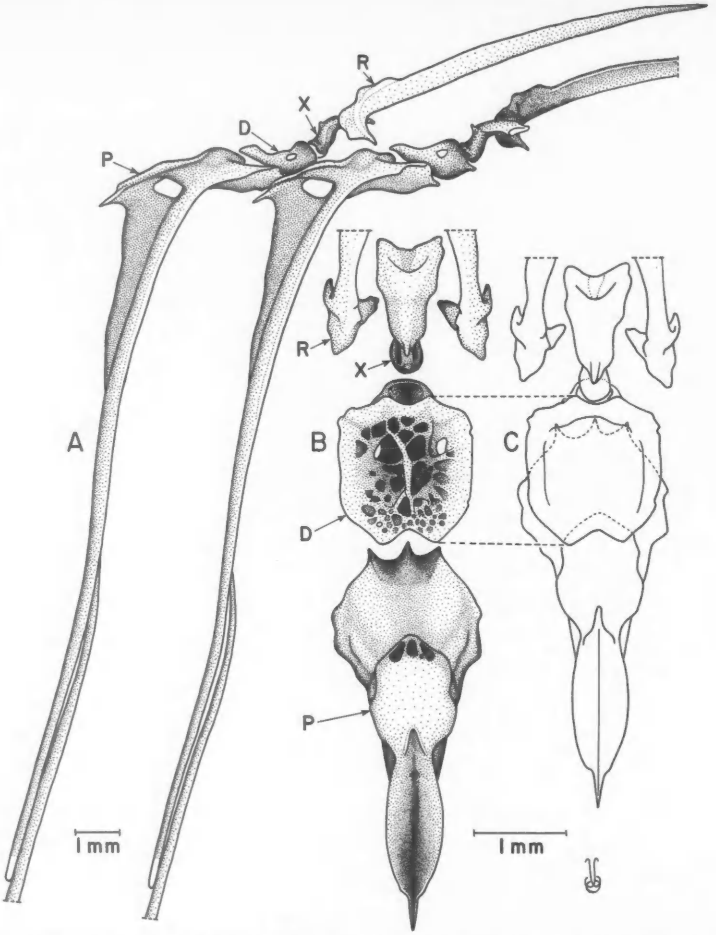

FIGURE 7.—Two dorsal fin pterygiophores from *Trichiurus lepturus* 510 mm TL, taken directly from opposite the anterior portion of the anal fin. A, left lateral view of the pterygiophores and rays; the left side of the posterior ray has been removed. Cartilage, white; ossifying, stippled. B, dorsal view of one of the two pterygiophores; unfused parts have been disarticulated. C, dorsal view of pterygiophore in B, unfused parts have been left articulated. For abbreviations see Figure 6.

broids (G. D. Johnson[3]). The anteriormost two dorsal pterygiophores supported three spines, which were the only dorsal fin spines and which had serrations in larvae and juveniles, but were smooth in adults. The anterior two pterygiophores had two parts each and supported fin spines. The 3d-127th pterygiophores had three parts and supported fin rays, the distal parts being located between the bifurcate bases of the rays. These distal parts were not homologous with distal radials and are labeled "X" in Figures 6-8. The 128th-130th pterygiophores had four parts, and the last three pterygiophores (131st-133d) had become vestigial having a variable number of parts, usually from two to four. Anal fin pterygiophores were anatomically similar to the dorsal fin pterygiophores. The first anal fin spine was large and serrated in larvae and juveniles but became small and smooth in adults. *Trichiurus* lar-

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[3] G. David Johnson, Curator (Fishes), Smithsonian Institution, National Museum of Natural History, Wash., DC 20560, pers. commun. 1985.

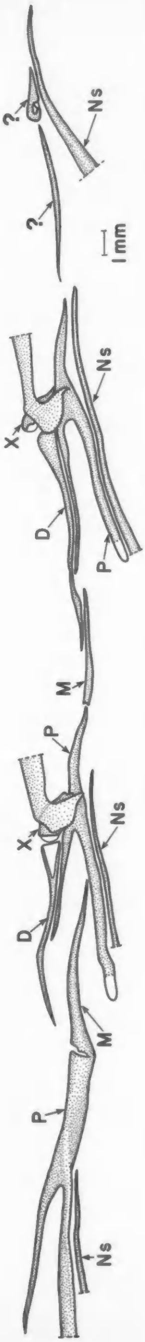


FIGURE 8.—Left lateral view of the three posteriormost dorsal fin pterygiophores from *Trichiurus lepturus* 303 mm TL. M, middle radial; ?, pterygiophore parts where homology cannot be determined; for other abbreviations see Figure 6. Cartilage, white; bone, stippled.

vae and juveniles developed an anal fin in which the rays were of the same length as those in the dorsal fin, but the anal rays became very short and vestigial in adults. In adult *Trichiurus* the posterior end of the dorsal fin was anterior to the posterior end of the anal fin. Other trichiurids (*Benthodesmus*, *Evoxymetapon*, *Lepidopus*) examined by us had pterygiophore arrangements similar to *Trichiurus*.

FAMILY SCOMBRIDAE

The family is a very speciose group which is divided into two subfamilies (Collette et al. 1984). For the monotypic Gasterochismatinae, larvae were not obtainable, but one or more species for each of the four tribes of the Scombrinae was studied.

Tribe Scombrini

Figure 9

Twenty-two *Scomber japonicus* (4.4 mm NL - 9.6 mm SL, 100, 103 mm SL) and 12 *S. scombrus* (5.7 mm NL - 8.2 mm SL) were used in this study. Many more *Scomber* smaller than 5.5 mm NL were available but showed no cartilage development along the notochord. In addition, developmental studies on *Scomber* by Kramer (1960) and Kohno et al. (1984) were consulted.

Development of the vertebral column in *Scomber* initially started in four places on the notochord: 1) posteroventrad (parhypural, hypurals 1 and 2), 2) ventrad at the center (anterior haemal arches and spines), 3) dorsad at the center (neural arches and spines above developing haemal arches and spines), and 4) anterodorsad (neural arches and spines of future centra 1-3). The anterior neural spines were added posteriorly, the neural spines at the center of the notochord were added anteriorly and posteriorly, the haemal spines were added posteriorly, but the parapophyses were added anteriorly. The hypurals were added in a posterior direction, but the two autogenous haemal spines were added anteriorly. The dorsal and ventral areas of development coalesced completing the cartilaginous ontogeny of the vertebral column. Ossification of the vertebral column (neural and haemal spines, vertebrae, and hypural complex) initially started in four places: 1) dorsoanteriorly (anteriormost neural arches and spines), 2) ventrad at the center (anterior haemal arches and spines and posterior parapophyses), 3) posteriorly (hypural complex), and 4) dorsad at the center (neural arches and spines). The four initial areas of ossification coalesced as ossification progressed. Vertebrae in *Scomber* initially had saddle-

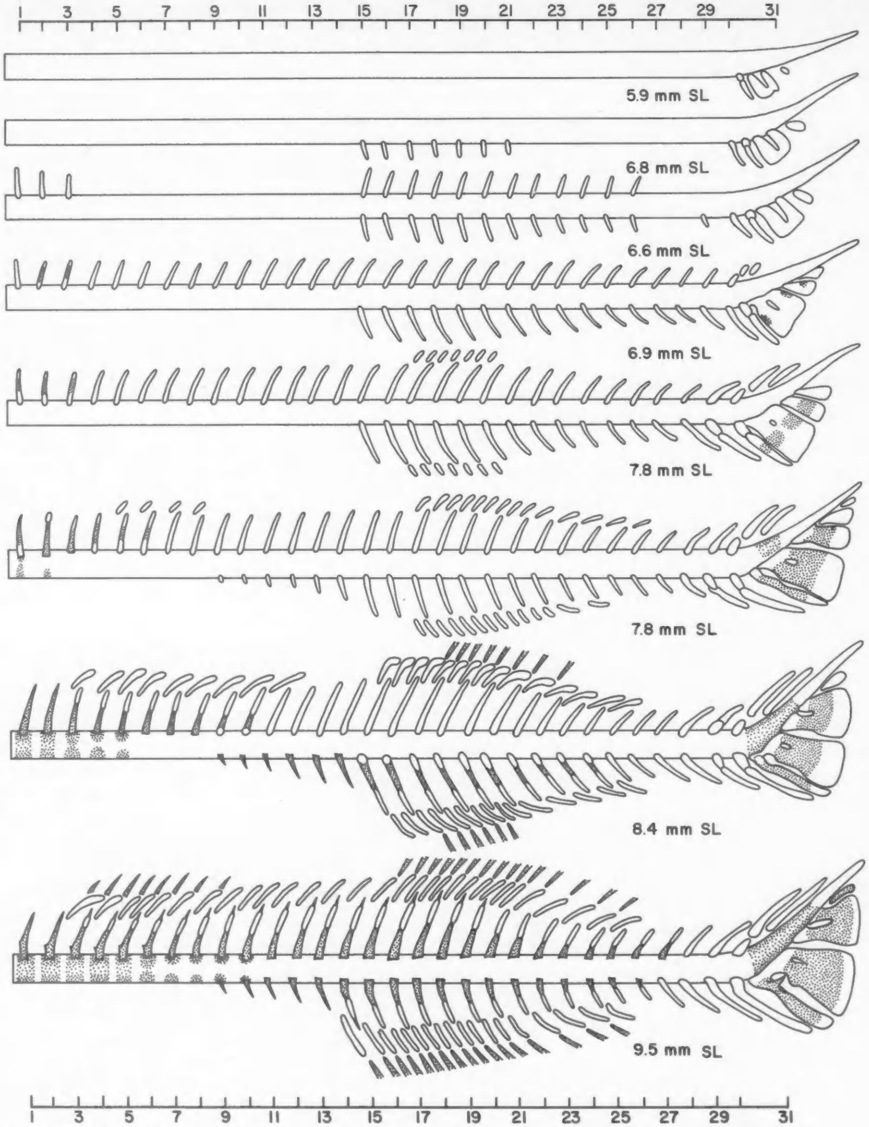

1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
5.9 mm SL
6.8 mm SL
6.6 mm SL
6.9 mm SL
7.8 mm SL
7.8 mm SL
8.4 mm SL
9.5 mm SL
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31

FIGURE 9.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scomber japonicus*, Scombrini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

Cartilaginous second dorsal and anal fin pterygiophores developed first simultaneously above interneural spaces and below interhaemal spaces 17-19. The addition of cartilaginous second dorsal and anal fin pterygiophores was in an anterior and posterior direction. Cartilaginous first dorsal fin pterygiophores appeared second above interneural spaces 5-8 and were added anteriorly and posteriorly, terminating anteriorly in the third interneural space and joining with the second dorsal fin pterygiophores posteriorly. Second dorsal and anal fin rays developed in the same sequence as their corresponding pterygiophore, but a little later. The first dorsal fin spines developed from anterior in a posterior direction, but the anteriormost (supernumerary) spine first developed when seven first dorsal fin spines were already present (Table 2).

Scomber lacked predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore was considerably larger than all other pterygiophores, but it originated from only one piece of cartilage supporting two anal spines (one supernumerary spine). The posteriormost six dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a posteriorly bifurcated stay (Table 1).

In *Scomber*, caudal development of the cartilaginous parhypural and hypurals 1 and 2 was first before any other development of cartilaginous haemal or neural arches and spines along the notochord. The development of the hypural complex from the first appearance of cartilaginous hypurals to ossification onset was described by Kohno et al. (1984) and our findings are in agreement with theirs. Kramer (1960) described the ossification sequence in the hypural complex of *Scomber*. In our specimens, hypurals 1 and 2 were fusing to a ventral hypural plate before ossification onset. Hypurals 3 and 4 were fusing in some larvae before and in others after ossification onset. The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. A procurrent spur and a basally foreshortened ray were absent in *Scomber* (Johnson 1975) (Table 1).

Tribe Scomberomorini

Figures 10, 11

Thirty-nine specimens were available: 9 *Scomberomorus cavalla* (4.1-6.2 mm NL), 17 *S. maculatus* (6.1 mm NL - 10.2 mm SL, 40.5-67.5 mm SL), 3 *S. regalis* (5.3, 6.5 mm NL, 85.0 mm SL), 4 *S. tritor* (6.0 mm NL - 8.0 mm SL), 6 *Acanthocybium solanderi* (6.2 mm NL - 10.8 mm SL). None of the above five species yielded complete developmental series. However, *S. cavalla* specimens showed the cartilaginous ontogeny of the vertebral column, of the dorsal and anal fin pterygiophores and of the hypural complex. The *S. maculatus* specimens showed the latter phases of pterygiophore and hypural complex development, dorsal and anal fin development, and the ossification of the vertebral column and the hypural complex. Specimens of *S. regalis* and *S. tritor* provided evidence that development for the Atlantic species of *Scomberomorus* is very similar. Specimens of *A. solanderi* gave incomplete information on cartilaginous vertebral column development, but adequate information on dorsal and anal pterygiophore, on dorsal and anal fin, on hypural complex development, and on the ossification sequence of the vertebral column.

Development of the vertebral column in *Scomberomorus* initially started in four places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1-3), 2) posteroventrad (parhypural, hypurals 1 and 2), 3) ventrad at the center (four haemal arches and spines), and 4) dorsad at the center (six neural arches and spines above initial haemal spine development). The anterior neural spines were added posteriad, the neural spines at the center of the notochord were added anteriorly and posteriorly, the haemal spines were added mostly posteriorly but a few were added in an anterior direction. All parapophyses were added in an anterior direction. The hypurals were added in a posterior direction, but the two autogenous haemal spines were added in an anterior direction. The dorsal and ventral areas of development coalesced and thus cartilaginous ontogeny of the vertebral column was complete. Ossification of the vertebral column initially started in two places: 1) anteriorly (neural arches and spines, and centra) and 2) posteriorly (hypural complex). Ossification of the neural arches and spines and centra was in a posterior direction. In the hypural complex ossification started with the urostyle and proceeded anteriorly to preural centrum 3. Then the ventral hypural plate started to ossify followed by the dorsal plate, the parhypural, and the two autogenous haemal spines. Last to start ossification were the epurals, the uroneural, and the neural spines. Vertebrae in *Scomberomorus* had saddle-shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

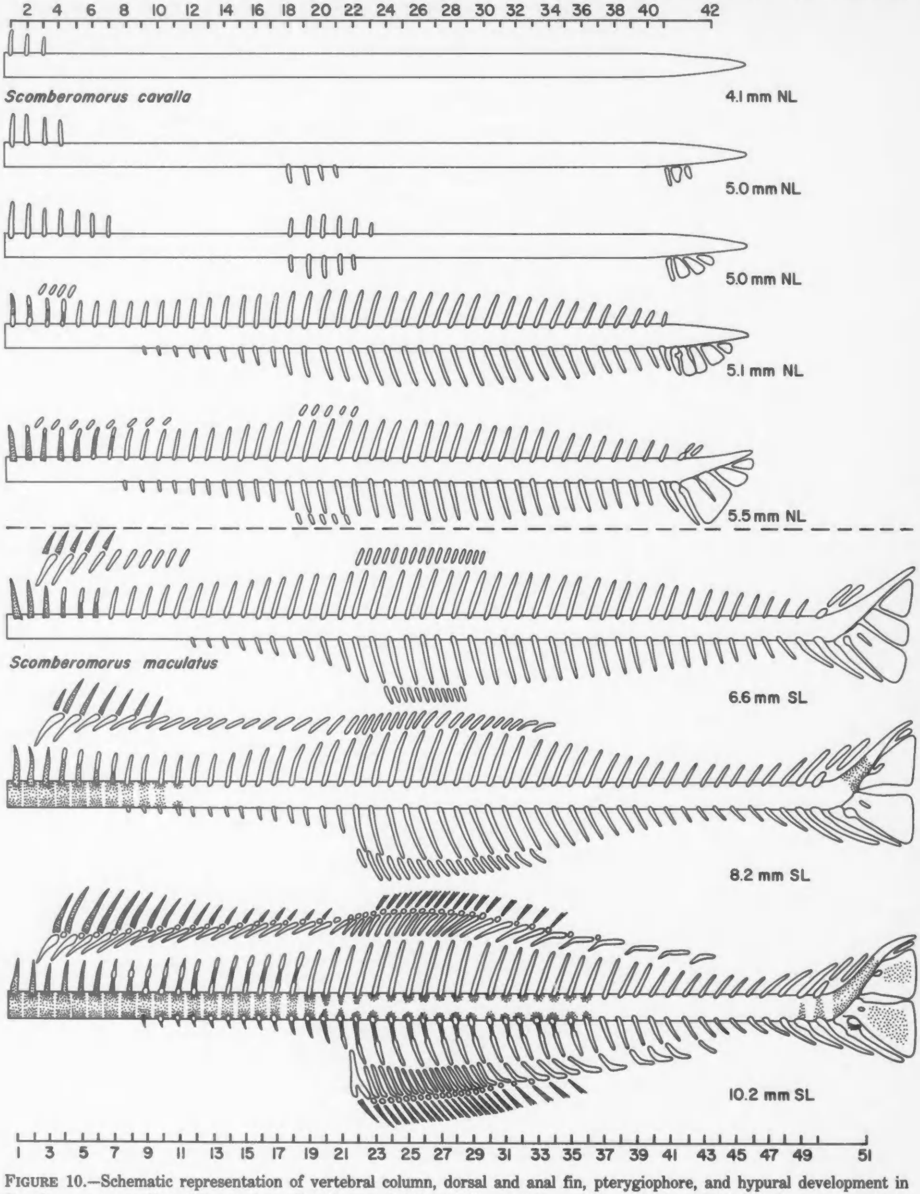

2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Scomberomorus cavalla
4.1 mm NL
5.0 mm NL
5.0 mm NL
5.1 mm NL
5.5 mm NL
Scomberomorus maculatus
6.6 mm SL
8.2 mm SL
10.2 mm SL
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51

FIGURE 10.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scomberomorus cavalla* and *S. maculatus*, Scomberomorini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

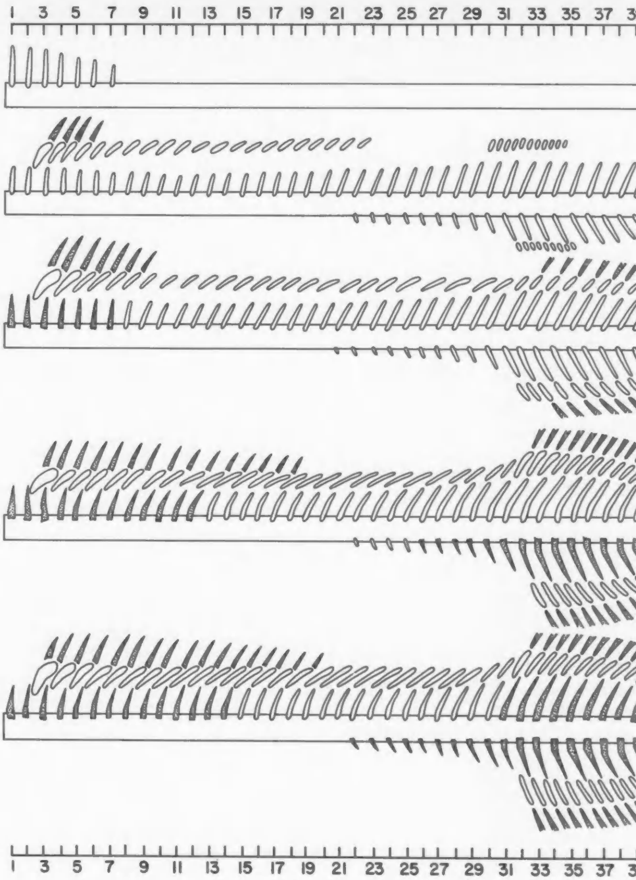
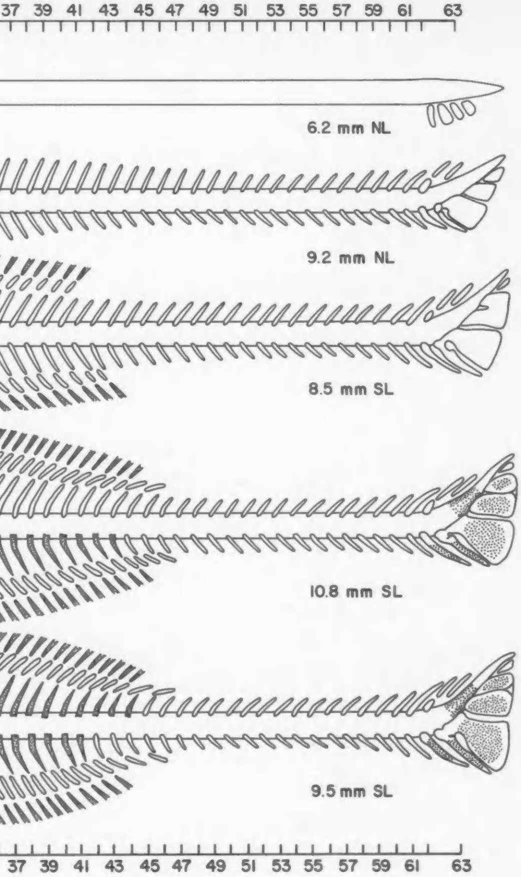

1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37

FIGURE 11.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Acanthocybium solanderi*, Scomberomorini, Scombridae. Cartilage, white; ossifying, stippled.

Scale repre
number.


37 39 41 43 45 47 49 51 53 55 57 59 61 63
6.2 mm NL
9.2 mm NL
8.5 mm SL
10.8 mm SL
9.5 mm SL
37 39 41 43 45 47 49 51 53 55 57 59 61 63

e represents interneural and interhaemal space number and vertebra
ber.

Two to five cartilaginous first dorsal fin pterygiophores developed first above interneural spaces 3-5 at the time of ossification onset of the anteriormost neural arches and spines. The addition of cartilaginous first dorsal fin pterygiophores was in a posterior direction. Five cartilaginous second dorsal and anal fin pterygiophores developed second simultaneously in the anterior portions of the future second dorsal and anal fins. Some addition of cartilaginous second dorsal and anal fin pterygiophores occurred in an anterior direction, but most of the addition was posteriorly. Dorsal and anal fin rays and spines developed in the same sequence as their corresponding pterygiophores, but a little later (Table 2).

Scomberomorus does not develop predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three spines (two supernumerary spines). The posteriormost nine dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a nonbifurcated stay (Table 1).

In *Scomberomorus*, first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the anterior development of the neural spines and the central appearance of haemal spines. Hypurals 3-5 were added posteriorly, the two autogenous haemal spines anteriorly. Hypurals 1 and 2 and hypurals 3 and 4 fused before ossification onset to a cartilaginous ventral and dorsal hypural plate. The dorsal and ventral plates fused after ossification to a single hypural plate with a central notch (Collette and Russo 1984). Hypural 5 gradually fused with the paired uroneural forming an autogenous bone resembling a third epural and mistaken as such by Leccia (1958). Two epurals developed anterior to the uroneural-hypural 5. These epurals remained autogenous. The neural and haemal elements of preural centra 2, 3, 4, and 5 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in *Scomberomorus* (Johnson 1975) (Table 1).

Only six *Acanthocybium solanderi* were available. We were therefore unable to ascertain a complete developmental sequence. Our smallest 6.2 mm NL specimen had two cartilaginous development centers along the notochord: some neural spines and arches anteriorly and the parhypural, hypural 1-3 posteriorly. The next larger specimen 9.2 mm SL had all neural and haemal arches and spines developed, thus we were unable to tell if in *Acanthocybium* four initial centers (as in *Scomberomorus*) or only three centers (as in *Xiphias* and *Sarda*) of cartilaginous development along the notochord were present. In all our *Acanthocybium* specimens, hypurals 1 and 2 gradually fused before ossification onset to a ventral cartilaginous hypural plate. In the 8.5 mm SL *Acanthocybium*, hypurals 3 and 4 were fusing before ossification onset; in the larger 9.5 and 10.4 mm SL specimens hypurals 3 and 4 were ossifying while still separate. The dorsal and ventral hypural plates were fused in adults to one plate with a notch (Conrad 1938; Collette and Russo 1984) (Table 1). Ossification of the vertebral column initially started in four places and was similar to the ossification in *Scomber*.

The development of the dorsal and anal fins and their supporting pterygiophores in *Acanthocybium* was similar to that described in *Scomberomorus*.

Tribe Sardini

Figure 12

Ninety-nine *Sarda sarda* (2.4-9.0 mm NL or SL, 59-102 mm SL) were available. Of the larval specimens (2.4-9.0 mm NL or SL) only 32 were larger than 5 mm NL, and of these 10 were between 6.0 and 6.9 mm NL or SL, 6 were between 7.0 and 7.9 mm NL or SL, and 3 were larger than 8 mm SL. Thus, since development of the vertebral column in *Sarda* begins around 5 mm NL, only 32 specimens were useful to our study and they were too few to yield a complete developmental series. Our conclusions on Sardini development are not as well supported as for most other scombroids.

Development of the vertebral column in *Sarda* initially started in three places on the notochord: 1) anterodorsad (neural arch and spine of future centrum 1), 2) posteroventrad (parhypural, hypurals 1 and 2), and 3) ventrad at center (haemal arches and spines, parapophyses). The anterior neural spines were added in a posterior direction and the haemal spines probably first appeared when the corresponding neural spines developed above them at the center of the notochord. Our evidence, however, is only indirect, because one 7.5 mm NL specimen had 21 neural spines and no haemal spines, but our 8.1 mm SL specimen had all neural and haemal spines developed. The cartilaginous hypurals were added posteriorly, but we could not observe the anterior addition of the autogenous haemal spines, although we assume that it happens in *Sarda* as in other scombroids with tails. Ossification of the vertebral column in *Sarda* initially started in two places: anteriorly (neural arches and spines) and posteriorly

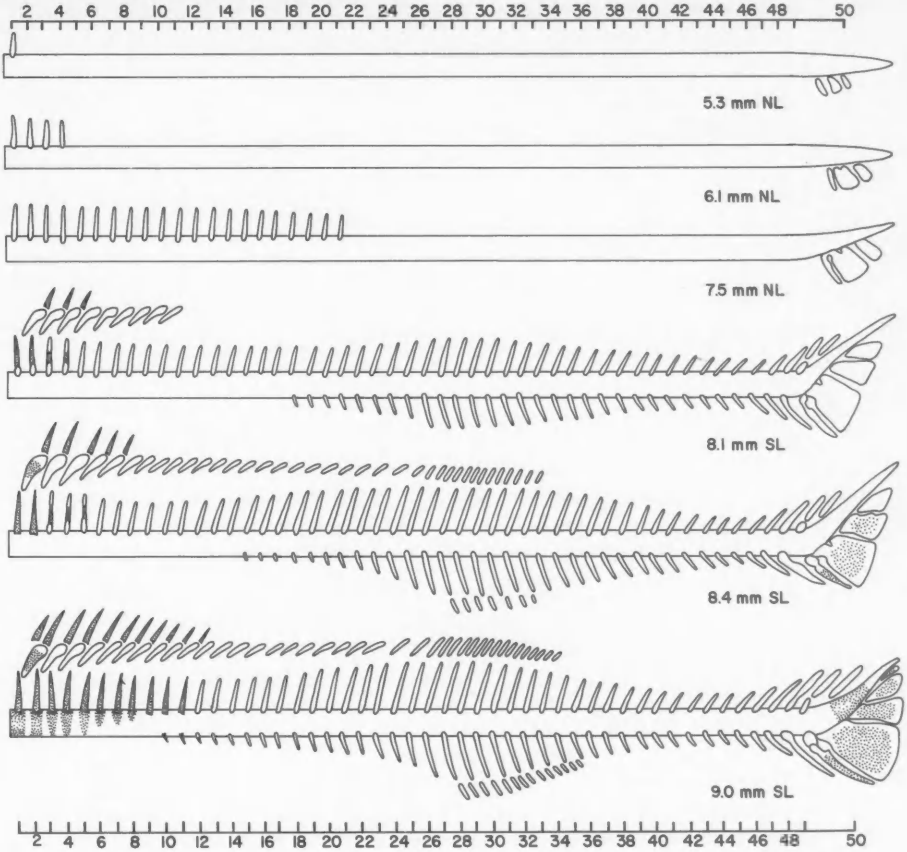


FIGURE 12.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Sarda sarda*, Sardini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

(hypural complex). Our largest 9.0 mm SL specimen showed ossification to the 11th neural spine. We do not know if ossification in *Sarda* proceeds entirely posteriad or if in *Sarda*, as in *Scomber* and *Acanthocybium*, there is some central ossification of neural and haemal spines before the anterior ossification has reached the center of the column. The hypural complex started to ossify early at the time ossification on the neural spines began anteriorly. Vertebrae in *Sarda* had saddle-shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

Cartilaginous first dorsal fin pterygiophores developed first anteriorly above interneural spaces 2-10 in the 8.1 mm SL specimen. Addition of cartilaginous first dorsal fin pterygiophores was in a posterior direction. The 8.4 mm specimen had all first dorsal fin pterygiophores and some second dorsal and anal fin pterygiophores and they were continuous with each other. Therefore, we are unable to determine if second dorsal and anal fin pterygiophores in *Sarda* developed before first dorsal fin pterygiophores were joined with the second dorsal fin pterygiophores. Three first dorsal fin spines were present in the 8.1 mm SL specimen, serially associated with the first three pterygiophores. Addition of first dorsal fin spines was in a posterior direction, except for the anteriormost first spine (supernumerary), which developed later in the 9.0 mm SL *Sarda*. Second dorsal and anal fin rays were not developed in our 9.0 mm SL specimen. Our 59 mm SL specimen had the full adult compliment of fin rays (Table 2).

Sarda did not develop predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the second interneural space supporting two spines (one supernumerary spine). We do not know if the first anal pterygiophore originated from one or two pieces of cartilage, but it is most likely that it originated from two pieces because it supported three fin elements (two supernumerary spines). The posteriormost seven to nine dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a posteriorly bifurcated stay (Table 1).

In *Sarda* first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the beginning development of the anteriormost neural arches and spines. Hypurals 1 and 2 fused in the cartilaginous state to form the ventral hypural plate. In three specimens, hypurals 3 and 4 were separate after ossification onset. These hypurals were fused to the dorsal hypural plate in juveniles. Hypural 5, the uroneural and two epurals were separate in our juveniles. Collette and Chao (1975) found that in adults the dorsal and ventral plates fused to one hypural plate without a notch and that the uroneural fused with hypural 5, but the two epurals remained autogenous. The neural and haemal elements of preural centra 2, 3, 4, and 5 supported the procurrent caudal rays. A procurrent spur and a basally foreshortened ray were absent in *Sarda* (Johnson 1975) (Table 1).

Tribe Thunnini

Figure 13

More than 86 specimens were available: 86 *Thunnus* (mostly *T. atlanticus* and a few *Thunnus* spp., 3.7-9.7 mm NL or SL), and a small number of *Auxis*, *Euthynnus*, and *Katsuwonus*. We were unable to observe early cartilaginous development in all genera except *Thunnus*.

Development of the vertebral column in *Thunnus* initially started in four places on the notochord: 1) anterodorsad (neural arches and spines of future vertebrae 1-3), 2) posteroventrad (hypurals 1 and 2), 3) ventrad at the center (anteriormost five haemal arches and spines and posteriormost two parapophyses), and 4) dorsad at the center (five neural arches and spines above initial haemal arch and spine development). The anterior neural arches and spines were added in a posterior direction, the central neural arches and spines were added anteriorly (coalescing around the future 14th centrum) and posteriorly toward the epurals. The parapophyses were added in an anterior direction, whereas the haemal arches and spines were developing in a posterior direction. In the hypural complex hypurals were added posteriorly, but the parhypural and the two autogenous haemal spines were added in an anterior direction, coalescing with the central haemal arches and spines. Ossification of the vertebral column in Thunnini initially started in two places similar to the ossification described for *Scomberomorus*. Saddle-shaped vertebral ossification development was observed in all Thunnini examined, similar to the development described for *Scombrolabrax* (Table 2).

In Thunnini, cartilaginous first dorsal fin pterygiophores developed anteriorly in interneural spaces 3-6 when only few cartilaginous neural spines were present. Additional pterygiophores were added in a posterior direction. Later, small cartilaginous second dorsal fin pterygiophores appeared in the middle of the vertebral column above interneural spaces 15-22. As the first dorsal fin pterygiophores developed in a posterior direction, the second dorsal fin pterygiophores developed in an anterior and posterior direction until all the dorsal pterygiophores were continuous. Anal pterygiophores appeared below interhaemal spaces 20-25 and developed in an anterior and posterior direction. Addition of the first dorsal fin spines was in a posterior direction, except for the anteriormost spine (supernumerary), which developed when the second and third spine were already present. The second dorsal and anal fin rays developed in the same sequence as their corresponding pterygiophores but a little later (Table 2).

All Thunnini species examined lacked predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three fin spines (two supernumerary spines) (Potthoff 1975). Middle radials were present on the posterior eight or nine finlet supporting dorsal and anal pterygiophores. A one-part posteriorly bifurcated stay developed with the posteriormost dorsal and anal fin pterygiophores (Table 1).

In *Thunnus*, the caudal complex began to develop very early concurrently with the first anteriormost neural spines. Hypurals 1 and 2 and hypurals 3 and 4 developed separate cartilages and fused to a cartilaginous dorsal and ventral hypural plate. Potthoff (1975) stated that hypurals 1 and 2 developed as one piece of cartilage from the start, but he examined only specimens larger than 5.0 mm NL not stained for cartilage. The dorsal and ventral hypural plates

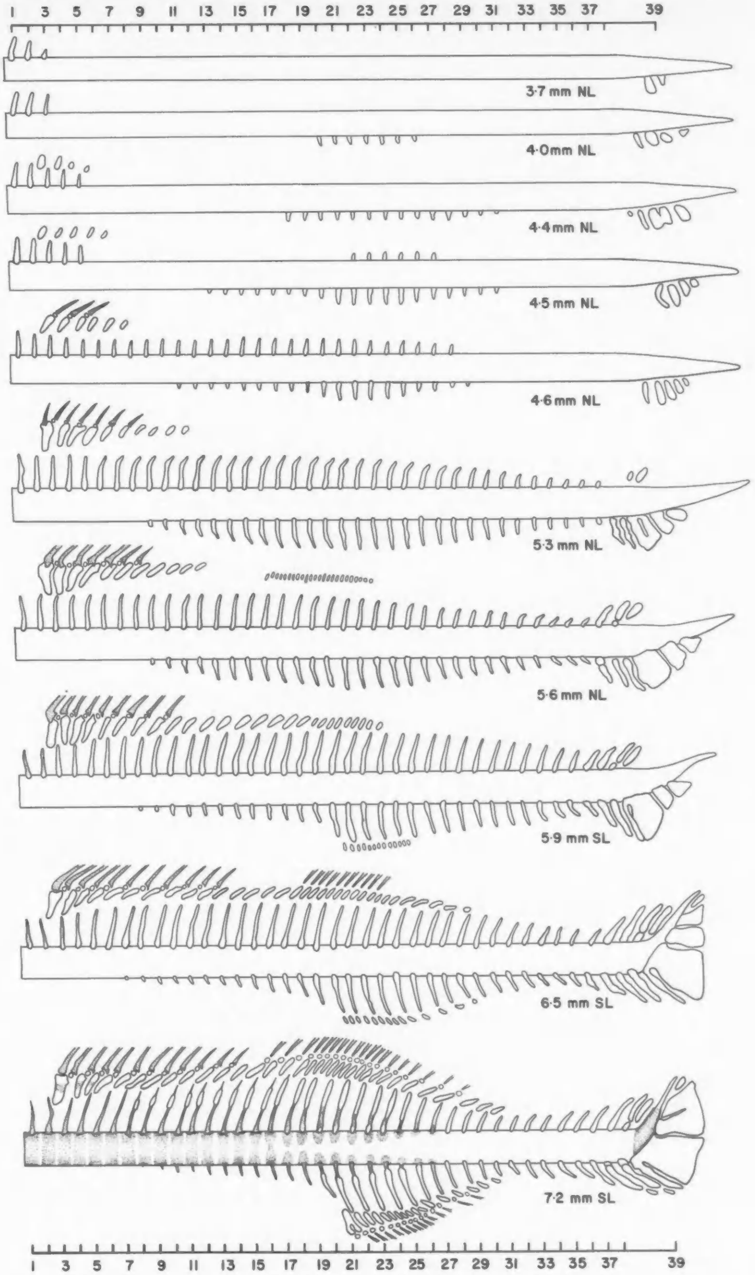

1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39
3·7 mm NL
4·0mm NL
4·4mm NL
4·5 mm NL
4·6mm NL
5·3 mm NL
5·6 mm NL
5·9 mm SL
6·5 mm SL
7·2 mm SL
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39

FIGURE 13.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Thunnus atlanticus*, Thunnini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

fused after ossification, but the small hypural 5 remained separate. Preural centra 2 and 3 each had an autogenous haemal spine. Two epurals and one uroneural developed dorsad. The anterior epural fused with the neural arch of Pu_2 and the uroneural fused to the urostyle (Potthoff 1975). The neural and haemal elements of preural centra 2, 3, and 4 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in the Thunnini (Johnson 1975) (Table 1).

FAMILY ISTIOPHORIDAE

Figure 14

One hundred and sixteen istiophorids (3.0-227 mm NL or SL) were available. Most specimens were caught in the Gulf Stream off Miami, FL. In 67 of the specimens we were able to count vertebrae; all had a count of 12 + 12. This identified them as *Istiophorus platypterus* or *Tetrapturus* spp. (Merrett 1971; Richards 1974). The 67 specimens with the 12 + 12 vertebral count, and the remainder, which were too small for vertebral counts, probably were *I. platypterus* because most adult istiophorids captured in the Gulf Stream off Miami are that species. In addition, 12 *Makaira nigricans* (3.3-5.9 mm NL, 13.3 and 220 mm SL) identified by W. J. Richards[4] were examined. The 13.3 and 220 mm SL specimens had a count of 11 + 13 vertebrae.

Development of the vertebral column initially started in three places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1 and 2), 2) posteroventrad (hypurals), and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were added in a posterior direction. The haemal arches and spines also were added in a posterior direction at the time when neural arches and spines appeared above on the notochord. Parapophyses were added anteriorly. Hypural bones were added in a posterior direction, but the parhypural and the two autogenous haemal spines were added anteriorly. Ossification of the vertebral column in istiophorids initially started in two places: ossification of the anteriormost neural spines and arches proceeded in a posterior direction. The hypural complex started ossification before all neural and haemal spines were ossifying. Saddle-shaped ossifications of the vertebrae as observed in the Scombrolabracidae, Gempylidae, and Scombridae were not observed in the Istiophoridae during ontogeny. First ossification of vertebrae in Istiophoridae was evidenced by the formation of rings of bone around the notochord (Table 2).

Cartilaginous dorsal pterygiophores appeared first above interneural spaces 3-5. Dorsal pterygiophore addition was mostly in a posterior direction, except that those pterygiophores over interneural spaces 2 and 1 were added in an anterior direction. When dorsal pterygiophore development extended to above the anterior portion of the anal fin fold, cartilaginous anterior anal pterygiophores were seen below interhaemal spaces 13 and 14, and their addition was posteriorly abreast of the dorsal pterygiophores. At larger sizes dorsal and anal finrays developed in the same sequence as their supporting pterygiophores (Table 2).

Istiophorids did not have predorsal bones, instead the first three interneural spaces were filled with fin spine supporting pterygiophores. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the first interneural space supporting three spines (two supernumerary spines). The anteriormost spine was either small, reduced, or vestigial. The first anal pterygiophore developed from two pieces of cartilage supporting two fin spines (one supernumerary spine). Istiophorids had one middle radial and one posteriorly bifurcated (sometimes nonbifurcated) stay with the posteriormost dorsal and anal pterygiophore. The posteriormost dorsal and anal ray were double (Table 1).

In istiophorids, the caudal complex started to develop after the precaudal neural spines had developed. The parhypural and hypurals 1-4 developed as separate cartilages. In most istiophorid specimens the cartilages of hypurals 1 and 2 and hypurals 3 and 4 fused to a lower and upper hypural plate before ossification; in some specimens fusion did not take place until after ossification onset for the upper and lower hypurals. Also, there were specimens in which none of the cartilaginous hypurals fused. The 5th hypural did not develop in istiophorids. Dorsad 3 epurals and 1 uroneural developed. Preural centra 2 and 3 each had one autogenous haemal spine. In adult istiophorids, the fusion of the bones in the caudal complex was extensive (Gregory and Conrad 1937); we examined adult specimens of *Istiophorus*, *Tetrapturus*, and *Makaira* and found identical hypural fusions in the three genera. The three epurals remained autogenous, but the uroneural, hypurals 1-4, and the parhypural were fused with each other and with the urostyle to form a notched hypural plate. The neural and haemal

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[4] W. J. Richards, Senior Scientist, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. 1983.

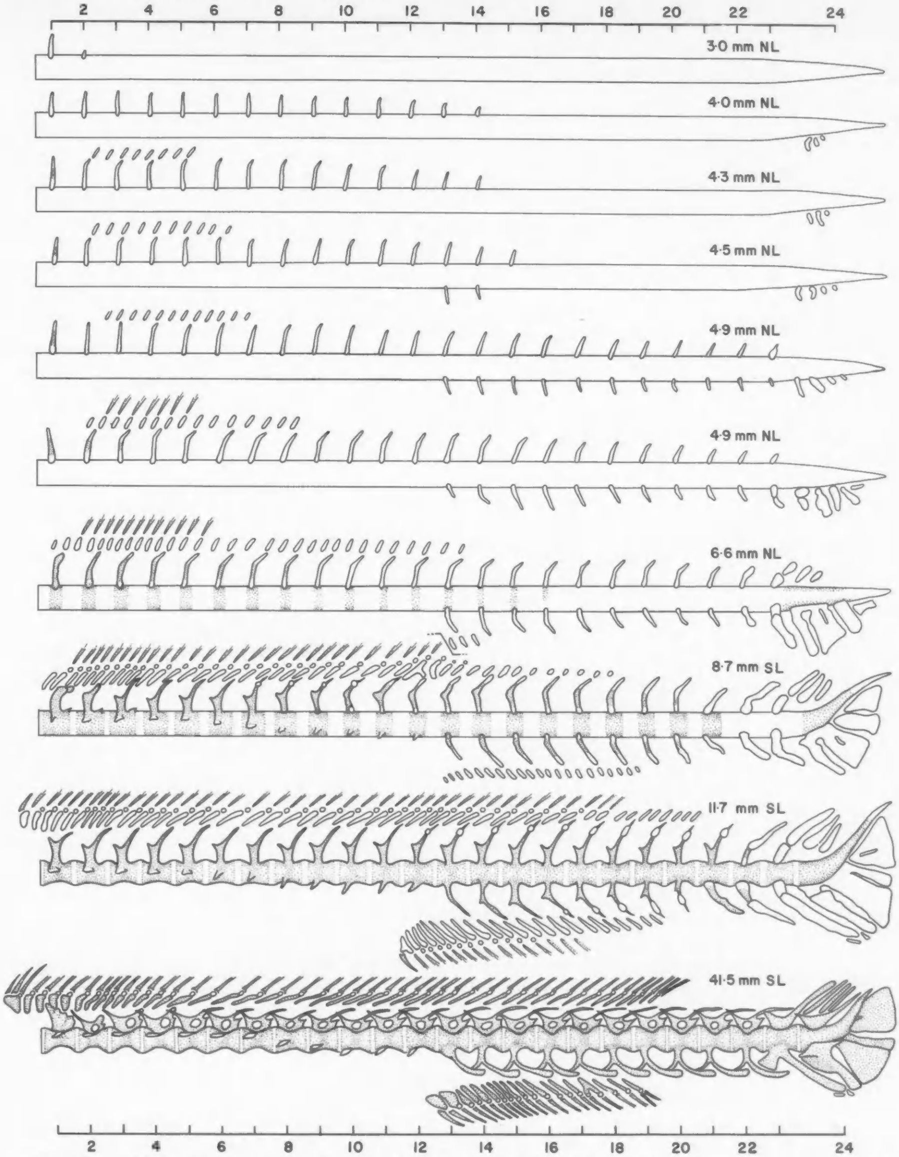
2
4
6
8
10
12
14
16
18
20
22
24
3·0 mm NL
4·0 mm NL
4·3 mm NL
4·5 mm NL
4·9 mm NL
4·9 mm NL
6·6 mm NL
8·7 mm SL
11·7 mm SL
41·5 mm SL

FIGURE 14.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Istiophorus platypterus*, Istiophoridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

elements of preural centra 2 and 3 supported procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in the Istiophoridae (Johnson 1975) (Table 1).

FAMILY XIPHIIDAE

Figure 15

Ninety-five *Xiphias gladius* specimens (3.7-19.5 ENL or ESL) of this monotypic genus and species studied by Potthoff and Kelley (1982) were reexamined by us.

Development of the vertebral column initially started in three places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1-3), 2) posteroventrad on the notochord (hypurals), and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were added in a posterior direction. When the developing neural spines had passed the precaudal area, some of the anterior haemal spines started to develop (except the anteriormost two of the future caudal vertebrae). Addition of cartilaginous neural and haemal spines was in a posterior direction, except the first two haemal spines which developed anteriorly. Hypural complex bones were added in an anterior and posterior direction. Ossification of the vertebral column in *Xiphias* initially started in one place with the anteriormost neural arches and spines. Ossification then proceeded in a posterior direction with the hypural complex ossifying last. Saddle-shaped ossifications of the vertebrae as observed in the Scombrolabracidae, Gempylidae, and Scombridae was not observed in *Xiphias* during ontogeny. Instead, vertebral ossification was first noted in *Xiphias* by the appearance of dorsoventral fractures on the notochord followed by the appearance of ossified vertebrae between the fractures (Table 2).

Cartilaginous dorsal and anal pterygiophores developed simultaneously before the neural and haemal spines had reached the area. The dorsal pterygiophores first developed in a group below the future middle of the dorsal fin above the future inter-

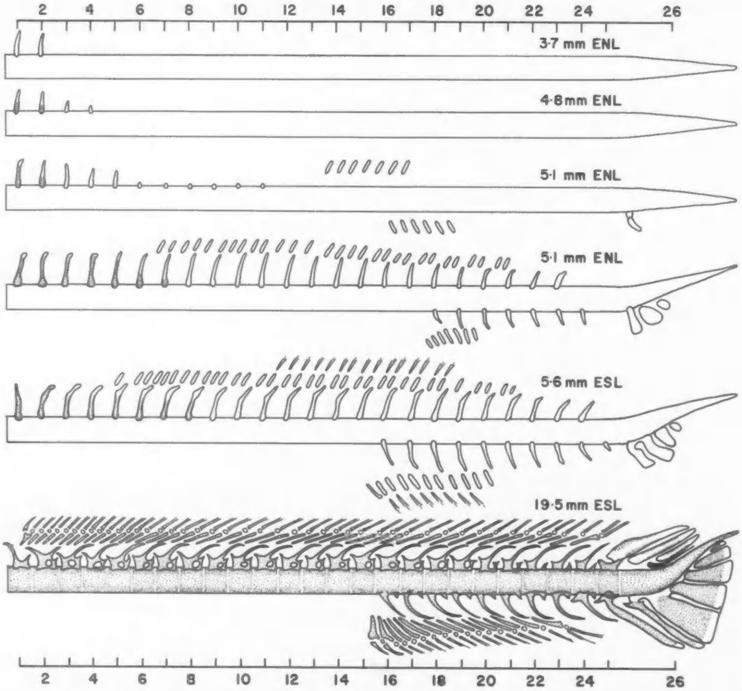

FIGURE 15.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Xiphias gladius*, Xiphiidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

neural spaces 13-16. The anal pterygiophores first developed in a group above the future anterior part of the anal fin below interhaemal spaces 16-18. Further addition of cartilaginous dorsal and anal pterygiophores was in an anterior and posterior direction. The posterior pterygiophore additions dorsad and ventrad were completed before the anterior additions ceased. The full complement of anal pterygiophores was reached before the full dorsal complement. Dorsal and anal fin rays first originated in the same areas as the pterygiophores, but at larger sizes with addition of rays in the same directions (Table 2).

Xiphias did not have predorsal bones. The first dorsal pterygiophore originated from one or two pieces of cartilage and inserted in the second interneural space, supporting from one to three fin spines. The first anal pterygiophore developed from one or two pieces of cartilage, supporting from one to three fin spines. *Xiphias* had no middle radials in the dorsal or anal pterygiophores, but a double ray and a nonbifurcated stay were associated with the posteriormost dorsal and anal pterygiophores (Potthoff and Kelley 1982) (Table 1).

In *Xiphias*, cartilaginous hypurals were first seen before precaudal neural spine development was complete, but after dorsal and anal pterygiophore development had started. The hypural complex development was described by Potthoff and Kelley (1982). Hypurals 1-5 and the parhypural developed from separate cartilages, and there was no cartilage fusion. There were three epurals and one uroneural. Only one autogenous haemal spine was present on preural centrum 2. In adults the three epurals, the uroneural, hypural 5, and the parhypural remained autogenous, but hypurals 1-4 fused with each other and the urostyle forming a notched hypural plate (Gregory and Conrad 1937). The neural and haemal elements of only preural centrum 2 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in *Xiphias* (Johnson 1975) (Table 1).

DISCUSSION AND CONCLUSION

Developmental features observed in our study are illustrated in Figures 4-5 and 9-15. These features along with meristic and osteological characters are compared among the six scombroid families and the primitive percoid *Morone* in Tables 1 and 2. Although our conclusions are still preliminary because of lack of adequate developmental series for many genera, some comparisons, based largely on development, are worth noticing.

There are three major kinds of early development and addition of the cartilaginous neural and haemal arches and spines along the notochord. Each kind may differ slightly between taxa. *Scombrolabrax*, *Scomber* (Scombrini), *Scomberomorus* (Scomberomorini), and Thunnini have one kind in which there are four initial developments on the notochord, but not necessarily in the given order, e.g., anteriorly dorsad, centrally dorsad, centrally ventrad, and posteriorly ventrad with a subsequent merger of the initial areas. Gempylidae, *Sarda* (Sardini), Istiophoridae, and Xiphiidae have a second kind in which there are three initial developments, e.g., anteriorly dorsad, centrally ventrad, and posteriorly ventrad; then the addition is from anterior in a posterior direction with a merger in the posterior, near the hypural complex. *Trichiurus*, which lacks hypurals, has the third kind in which there are two initial developments, e.g., anteriorly dorsad and centrally ventrad with addition in a posterior direction. We could not fully determine the cartilaginous development for *Acanthocybium*, because of an incomplete series, and for trichiurids with tails, because a series was lacking.

In the Scombrolabracidae, Gempylidae, and Scombridae, the vertebrae first develop by coalescence of saddle-shaped ossifications positioned dorsad and ventrad. We were not able to observe saddle-shaped ossification in *Acanthocybium* because we lacked specimens. The other scombroid families, Trichiuridae (*Trichiurus*), Istiophoridae, and Xiphiidae, and the primitive percoid *Morone* did not have these saddle-shaped ossifications. Saddle-shaped ossifications have been observed during ontogeny in other perciform fish such as *Enchelyurus brunneolus* (Blenniidae) by Watson[5] and *Lutjanus campechanus* (Lutjanidae) by Potthoff and Kelley[6]. We are unable to comment at this time on the significance of these saddle-shaped ossifications until the ontogeny of many more taxa is studied.

In the Scombrinae two species belonging to two different tribes share a peculiar ossification sequence not observed by us in any other scombroids. Both in *Scomber* (Scombrini) and *Acanthocybium* (Sardini), initial ossification of the neural and haemal arches and spines and the hypural complex started at four locations on the vertebral column (Kramer

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[5] Watson, W. Larval development of *Enchelyurus brunneolus* from Hawaiian waters (Pisces: Blennidae: Omobranchini). Unpubl. manuscr. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Soloma Beach, CA 92075.

[6] Research on the development of *Lutjanus campechanus* is in progress at the Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

1960). In other scombroids initial ossification was only anterior and posterior (*Scomberomorus*, *Sarda* ?, *Thunnus*, Istiophoridae) or only anterior (*Scombrolabrax*, Gempylidae, *Trichiurus*, *Xiphias*). We believe that the relationship of *Acanthocybium* to the Sardini should be re-examined in the future.

The Scombrini and *Scombrolabrax* (Figs. 1, 9) share a primitive development in which the second dorsal fin, anal fin, and pterygiophores develop first from a center anteriorly and posteriorly, and the first dorsal fin and pterygiophores develop second, from a center anteriorly and posteriorly in *Scombrolabrax*, but posteriorly only in *Scomber* except for the first dorsal fin spine, which was added later. The Gempylidae, Thunnini, and *Scomberomorus* (Figs. 2, 3, 4, 10, 13) share an advanced development in which the first dorsal fin and pterygiophores develop first from the anteriormost element in a posterior direction, and the second dorsal fin, anal fin, and pterygiophores develop second from a center anteriorly and posteriorly, the first dorsal fin being separate from the second dorsal fin during part of the ontogeny. In *Acanthocybium*, *Sarda*, and Thunnini, the development is similar to the advanced development of the Gempylidae and *Scomberomorus* except in *Acanthocybium*, *Sarda*, and Thunnini, the second dorsal fin spine developed first, the first dorsal fin spine was added later. The first dorsal fin was separate for part of the ontogeny from the second dorsal in *Acanthocybium*, but we were unable to observe this in *Sarda* because of the lack of an adequate size series. In *Trichiurus* (Fig. 5), the dorsal fin and pterygiophores develop from the anteriormost element posteriorly. When dorsal fin development reaches above the anal fin, the anal fin develops from its anteriormost element in a posterior direction. Dorsal and anal fin development then proceed posteriorly at about the same pace. *Trichiurus* has a peculiar developmental feature, which was not observed in any other scombroid. It was that the anteriormost dorsal fin spines and anal spine and rays develop before their corresponding pterygiophores. Pterygiophore development soon overtook fin ray development and during further development more pterygiophores are present than fin rays. In the Istiophoridae and Xiphiidae, dorsal and anal fin development differ from the previously described groups. In the Istiophoridae (Fig. 14) the first dorsal fin and pterygiophores develop first from a center anteriorly and posteriorly. When the posterior portion of the first dorsal fin development reaches above the anterior portion of the anal fin, anal rays and pterygiophores are added mostly posteriorly, although a few elements develop in an anterior direction. The second dorsal fin develops only in a posterior direction consecutive to the first dorsal fin. In *Xiphias* (Fig. 15), the second dorsal and anal fins and pterygiophores develop first from a center anteriorly and posteriorly. Development of the first dorsal fin and pterygiophores then is continuous with the second dorsal fin in an anterior direction only.

The hypurals in all scombroids develop as separate cartilages. Only in *Scombrolabrax* is there no fusion of the hypurals in the adults. In the Gempylidae the extent of the hypural fusion varies for different genera and we did not observe fusion in the cartilaginous state. For the trichiurids with tails, not enough specimens were available to make observations on hypural fusion. In the remaining scombroids (Scombridae, Istiophoridae, Xiphiidae) hypurals 1-4 are fused to one hypural plate in adults. Fusion to one hypural plate came about during ontogeny by fusion of hypurals 1 and 2 to a ventral and hypurals 3 and 4 to a dorsal hypural plate, with subsequent fusion of these into one plate. For the ventral plate, cartilaginous fusion occurs in all tribes of the Scombridae, but in the Istiophoridae fusion is either from cartilaginous or ossifying hypurals 1 and 2 and in *Xiphias* it is always from ossifying hypurals (Table 1). In *Scomber*, *Acanthocybium*, and Istiophoridae, the fusion of hypurals 3 and 4 to the dorsal hypural plate is variable and occurs either during the cartilaginous or ossifying state. In *Sarda* three specimens have fusion of hypurals 3 and 4 in the ossifying state. In *Scomberomorus* and *Thunnus* the fusion to the dorsal hypural plate occurs always in the cartilaginous state, whereas in *Xiphias* it is always in the ossifying state (Table 1).

The number of centra supporting the caudal rays varies in the scombroids. In *Scombrolabrax*, Gempylidae, Trichiuridae with tails, *Scomber*, and Istiophoridae, three vertebrae (including the urostyle) support the caudal rays. In *Xiphias* only two vertebrae support the rays. In the Scombridae more vertebrae are involved with the support of the caudal rays, except in *Scomber*. In the *Scomberomorus* species examined by us, five centra support the rays, but in some species of *Scomberomorus* only four centra are involved (Collette and Russo 1984). In *Acanthocybium* (Collette and Russo 1984) and *Sarda*, five centra are involved with the support of the rays, whereas in *Thunnus* only four centra support the caudal rays (Table 1).

Johnson (fn. 3; in press) is of the opinion that *Scombrolabrax* does not belong in the Scombroidei because it lacks most defining specializations of this group. Bond and Uyeno (1981) removed *Scombrolabrax* from the Scombroidei on the basis of one specialized character. We are of the opinion that *Scombrolabrax* should be retained in the Scombroidei until we fully understand the significance of developmental characters. *Scombrolabrax* shares many characters with other scombroids, in particular the absence of predorsal bones coupled with the anterior pterygiophore interneural insertion sequence, the saddle-shaped ossifications of the vertebrae, the sequence of neural and haemal arch and spine development and the striking resemblance of *Scombrolabrax* to Thunnini larvae.

Gempylid and trichiurid relationships await further study when complete series of larvae of more species become available. We believe that *Gempylus* and *Diplospinus* are similar and very closely related. We also believe that the gempylids and trichiurids are very closely related, the trichiurids representing an advanced gempylid group.

Johnson (in press) has discovered a specialization (a stay on the 4th pharyngobranchial) unique to the Scombridae, Istiophoridae, and Xiphiidae but absent in other Perciformes. From our study we believe that the billfish (*Xiphias* and Istiophoridae) do not belong in the Scombroidei because they differ in many developmental and meristic characters from other scombroid members (Tables 1, 2). However, until more developmental studies are done to determine the meaning and significance of developmental characters, it would be premature to suggest rearranging the Scombroidei.

The full value of early developmental studies for systematic purposes will be realized when similar studies have been completed on a greater variety of fishes. Only then will we be able to interpret the meaning and significance of some developmental characters presented here.

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AGE AND GROWTH OF THE MARINE CATFISH, *NETUMA BARBA* (SILURIFORMES, ARIIDAE), IN THE ESTUARY OF THE PATOS LAGOON (BRASIL)[1]

ENIR GIRONDI REIS[2]

ABSTRACT

Otolith cross sections from *Netuma barba* were used for age and growth determinations. There is close agreement between average back-calculated lengths and average observed lengths determined from otoliths at capture for each year class. One opaque and one hyaline zone is formed annually. The hyaline zone appears to be formed during the breeding season when the estuarine mature population is scarcely feeding. Von Bertalanffy growth parameters were estimated through Beverton's method which showed the smallest residual variance between observed and calculated lengths for year class. The growth equation (mm) is $Lt = 638\,[1 - \exp(-0.1287(t + 0.195))]$. The largest specimen observed was $\cong$ 980 mm female, 36 years old. The life span of *N. barba* was estimated to be 23.1 years and the natural mortality rate 0.13.

The sea catfish, *Netuma barba* (Lacepède 1803), ranges in the western Atlantic from Bahia (lat. 17°00′S) in Brasil (Günther 1864) to San Blas (lat. 40°32′S) Argentina (López and Bellisio 1965). It is the second most important estuarine fishery resource in the Patos Lagoon and is caught with gill nets (Reis 1982a). The species accounts for about 29% of the total fish landings in the estuary from October to December, a period when it migrates from the sea to spawn. During the remaining months the species is dispersed in low abundance in the ocean (Reis in press). Observations on *Netuma barba* in Brasil have been restricted to taxonomy (Higuchi et al. 1982) and to feeding and reproduction (Ihering 1888, 1896; Nomura and Menezes 1964; Reis in press).

Age determinations in catfishes are usually based on reading vertebrae and pectoral or dorsal spines (Pantulu 1962; Tweddle 1975). Pectoral spines of *Netuma barba* were not used in the present study because they showed inconsistencies in age determination. However, a preliminary investigation revealed the presence of clear and readable zones in otoliths. This paper deals with the interpretation of these zones, the possible causes of zone formation, and the determination of growth of *Netuma barba* in the estuary of the Patos Lagoon.

MATERIALS AND METHODS

Study Area

The Patos Lagoon, the largest lagoon system in southern Brasil (10,360 km^2), is connected to the Atlantic Ocean by a narrow access canal (Fig. 1). The estuary of the lagoon serves as a breeding, nursery, and feeding ground for most of the coastal fish which migrate through the canal and represent a significant percentage of the national fishery resource.

Collections of adult *Netuma barba* were made from fish-processing plants located in the estuarine zone of the lagoon, off the coast of Rio Grande to São Lourenço do Sul, a town located 94 km inland (Fig. 1). Juveniles were collected by special research surveys carried out in the estuary. Data were collected from September 1977 to December 1980 on 4,120 specimens. No samples were available from January to March because of a closed fishing season of Ariidae in the area, and few samples were collected from April to July due to the absence of the species in the estuary.

Sampling Procedure

Specimens were measured (total length, mm), weighed (g), and sexed. Lapillus otoliths were removed, sectioned transversally next to the nucleus, polished, and were examined under a 10× binocular microscope. The dorsal, polished half of the otoliths was observed with transmitted light. The

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[1] Based on a thesis in partial fulfillment of the requirements for the MS degree, Fundação Universidade do Rio Grande - Rio Grande (Brasil).

[2] Departamento de Oceanografia, Fundação Universidade do Rio Grande, Caixa Postal 474, 96200 - Rio Grande - RS, Brasil.

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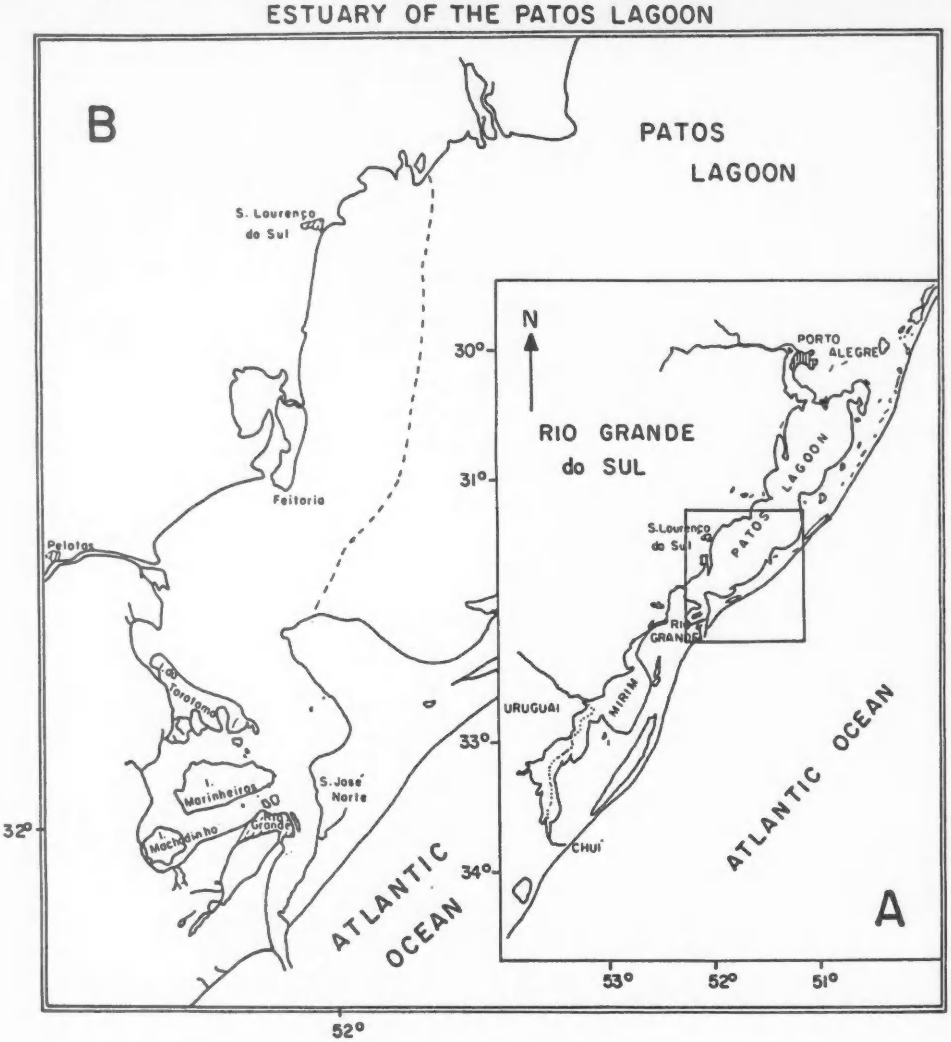
ESTUARY OF THE PATOS LAGOON
B
PATOS
LAGOON
S. Lourenço do Sul
Feitoria
Pelotas
I. da Torotama
I. Marinheiros
I. Machadinho
Rio Grande
S. José Norte
ATLANTIC OCEAN
32°
52°
30°
31°
33°
34°
N
RIO GRANDE do SUL
PORTO ALEGRE
PATOS LAGOON
S. Lourenço do Sul
RIO GRANDE
URUGUAI
MIRIM
CHUI
ATLANTIC OCEAN
A
53°
52°
51°

FIGURE 1.—Coastal lagoon system of southern Brasil (A) and the study area (B).

type of deposit (opaque or hyaline) on the otolith margin and the number of hyaline zones were recorded for each otolith. Back-calculation was done over the surface, the total length of the otolith (Co) and the length between the nucleus and each hyaline zone (ci) (Fig. 2) were measured with an ocular micrometer. The term nucleus used here refers to the central area of the otolith limited by the first zone (Jearld 1983).

Growth curves for males and females were calculated using the mean lengths for year class. The parameters of the von Bertalanffy growth equation were determined:

$$Lt = L_\infty [1 - e^{-K(t-t_0)}] \qquad (1)$$

where Lt is the total length at time t, L_∞ is the maximum attainable size, K is the growth coeffi-

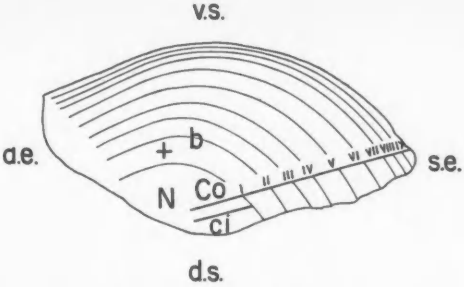

FIGURE 2.—A lapillus otolith of *Netuma barba* showing opaque (+) and hyaline (b) zones, the nucleus (N), the axes where back-calculation was made (Co = distance between the nucleus and the otolith's edge; ci = distance from the nucleus to "i" hyaline zone) and the position of otolith on fish head (a.e. = antisulcal end; s.e. = sulcal end; d.s. = dorsal surface; v.s. = ventral surface; and hyaline zones = I-IX).

cient, and t_0 a correction on the time axis. The parameters of Equation (1) were estimated by determining the predictive regression of $\ln(L_\infty - Lt)$ against t (Beverton 1954):

$$\ln(L_\infty - Lt) = \ln L_\infty + K(t_0 - t) \qquad (2)$$

where K is the slope of the regression line and the y-intercept of Equation (2) can be equated to $\ln L_\infty + Kt_0$ providing the value of t_0 (Ricker 1975). Trial plots, including values of L_∞ first derived by the methods of Walford (1946) and Gulland (1964), yielded the L_∞ which gives the straightest line. The agreement between observed and calculated lengths for year class was determined by residual variance (S^2y) expressed by

$$S^2y = \frac{\sum(\text{observed } Lt - \text{calculated } Lt)^2}{N - 1} \qquad (3)$$

where N is the number of age classes.

Length-weight relationship was determined for males and females

$$Wt = \mu Lt^v \qquad (4)$$

where Wt is the weight at time t, and μ and v the coefficients of the functional regression between Wt and Lt (Ricker 1973). The condition factor was calculated for each sex as follows:

$$K = \frac{Wt}{Lt^v} \qquad (5)$$

and

$$Wt = W_\infty [1 - e^{-K(t-t_0)}]^v \qquad (6)$$

expressed growth in weight, where W_∞ is the maximum attainable weight obtained by solving for L_∞ in Equation (4).

The life span was estimated:

$$A_{0.95} = t_0 - \frac{\ln(1 - P)}{K} \qquad \text{(Taylor 1960)} \quad (7)$$

where $A_{0.95}$ is the time required to attain 95% of L_∞, $P = 0.95$ and t_0 and K are derived from the growth equation. The natural mortality coefficient (M) was estimated according to Taylor (1960)

$$M = \frac{\ln(1 - P)}{A_{0.95}} \qquad (8)$$

Statistical analyses were done when necessary (Snedecor and Cochran 1970; Sokal and Rohlf 1981).

RESULTS AND DISCUSSION

Age Determination

The lapillus otolith used for the determination of age of *Netuma barba* is the most developed ear bone in the Ariidae (Stinton 1975), its length attaining 3% of fish fork length (Reis 1982b). Growth zones can be observed on a sectioned otolith from the sulcal to the antisulcal end and from the nucleus on the dorsal face to the ventral one (Fig. 2). The hyaline and opaque zones are clearly evident even in otoliths of old specimens. Under transmitted light the opaque zones, or fast-growth zones, are white (broad) and hyaline zones, or slow-growth zones, are dark (narrow) (Fig. 2). Warburton (1978) counted growth checks on whole otoliths of *Galeichthys caerulescens* (Günther), and Dmitrenko (1975) studied *Arius thalassinus* (Rüppel) by viewing the otoliths the same way as in the present paper. The number of hyaline zones on sectioned otoliths and of growth checks observed on whole otoliths (Warburton 1978) were compared. A smaller number of growth checks was encountered in all cases when using whole otoliths.

In the present study only 2.4% of the otoliths were considered illegible. About 60% agreement was obtained when otoliths were read on two different occasions separated by a month. Disagreement was due to the inability to distinguish the first hyaline zone and those near the otolith's edge. When the same otoliths were analyzed for the third time, the agreement between observations increased to 79.9%.

Time of Zone Formation

The percentage of hyaline and opaque edged otoliths was plotted for each month (Fig. 3). Otoliths showing hyaline edge are more abundant in December when they comprise 63.7% of the total; opaque edged otoliths are fewer in this month (33.9%). Student's *t*-test (Snedecor and Cochran 1970) showed that proportions between hyaline and opaque edged otoliths differ significantly ($P < 0.05$) for most months (Fig. 3). Also, the mean width of the opaque zone on the otolith edge decreased towards the end of the year (Fig. 4), indicating a recent hyaline zone formation. The period of zone formation is not the same for all individuals, the result of individual growth differences. It is evident, however, that only one hyaline and one opaque zone is formed each year. Formation of slow-growth zones during warm months in *Netuma barba* coincides with the spawning period and the cessation of feeding activity (Reis in press). Both events suggest a decrease or a pause in growth when hyaline zones are formed. Menon (1953) observed that decreased feeding and gonad maturation may cause a periodic formation of the growth marks in skeletal parts of fish. During the

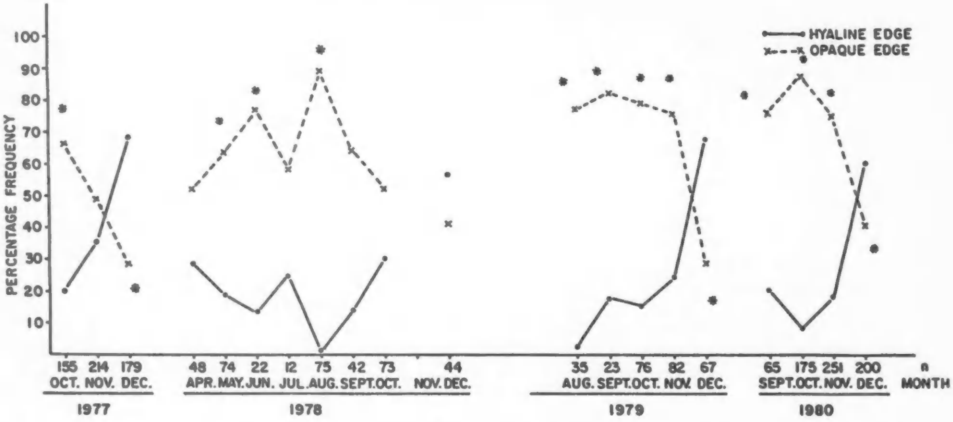

FIGURE 3.—Percentage of hyaline and opaque edge on otoliths of *Netuma barba* related to the months of four years (* $P < 0.05$; n = number of specimens).

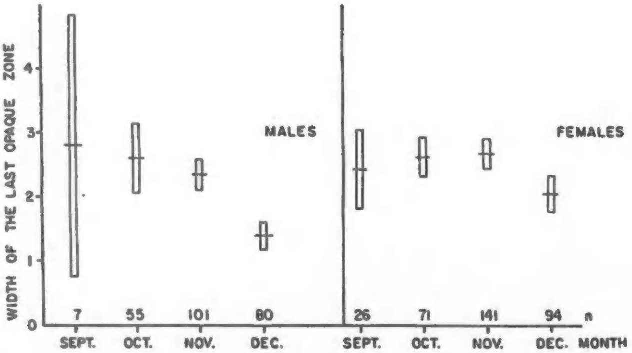

FIGURE 4.—Mean width and confidence limits at $P < 0.05$ level of the last opaque zone on otolith's edge for males and females of *Netuma barba* (n = number of specimens).

remaining months, when *Netuma barba* is at sea actively feeding and the gonads are resting (Reis in press), the opaque zones appear to be laid down due to fast somatic growth. According to Pannella (1974), fishes of temperate environments tend to form opaque zones or fast-growth zones during warm months but the synonymity of the terms summer and opaque, winter and hyaline has to be demonstrated in each instance rather than accepted as a general fact. For *Netuma barba* slow-growth zones are formed during warm months and may be related to the maturation of the gonads and a pause in feeding activity. Gonad maturation may be one of the causative factors of hyaline formation in adults; however, a plausible cause still needs to be established for immature specimens.

GROWTH

Growth in Length

Sectioned otolith lengths (measured as shown in Figure 2), and fish lengths were best fitted to the power curve:

$$Lt = 1.89\ \mathrm{Co}^{1.047} \qquad r = 0.960; \qquad n = 689,$$

and the equation for back-calculation was

$$Lt\ i = Lt\left(\frac{ci}{Co}\right)^{1.047}$$

where $Lt\ i$ is the length of fish when zone "*i*" was formed. Observed and back-calculated mean lengths for year class for each sex increase as one opaque and one hyaline zones are formed in the otolith each year (Table 1). Up to age 11, the mean lengths are similar; older females had mean lengths greater than males. The same was true for mean weight although a small number of specimens were analyzed from age 11 onward. Observed lengths are usually higher than back-calculated lengths except in ages that few specimens were analyzed.

Lengths corresponding to ages 8 to 12 are most frequent in the samples since they are most affected by the mesh size of the fishing gear used in the estuary. Mean observed lengths at these ages agree closely with mean back-calculated lengths (Fig. 5) for both sexes. Gill nets are highly size selective and retain fish at lengths of 370-520 mm (Reis 1982a). The analysis of variance (Sokal and Rohlf 1981) showed that observed lengths at ages 5, 6, and 7 are significantly higher than back-calculated lengths ($P < 0.05$) which could be due to the capture of the largest specimens of these ages since the minimum size of fish held by gill nets depends on the maximum body girth (opercle). Mean back-calculated lengths showed no definitive tendencies for any age class (Fig. 6) indicating no growth changes. Fur-

TABLE 1.—Mean observed and back-calculated lengths of males and females of *Netuma barba* for each age class (sample size in parentheses).

Estimated age	Mean observed length		Mean back-calculated length	
	Male	Female	Male	Female
1	84 (10)	96 (4)	65 (310)	63 (370)
2	145 (31)	152 (21)	140 (303)	137 (371)
3	203 (40)	197 (50)	193 (295)	192 (362)
4	228 (7)	261 (2)	244 (291)	245 (359)
5	348 (16)	146 (1)	300 (286)	299 (357)
6	378 (28)	365 (11)	347 (281)	347 (349)
7	403 (59)	394 (56)	386 (263)	385 (336)
8	415 (144)	416 (111)	413 (241)	412 (313)
9	433 (291)	431 (281)	430 (140)	433 (193)
10	452 (94)	463 (120)	444 (79)	446 (129)
11	476 (73)	493 (138)	455 (31)	462 (54)
12	490 (57)	526 (51)	460 (8)	507 (8)
13	464 (15)	602 (23)	508 (4)	612 (3)
14	551 (10)	667 (21)	480 (3)	637 (2)
15	522 (13)	622 (5)	520 (2)	578 (1)
16	533 (10)	620 (3)	528 (1)	608 (1)
17	494 (2)	647 (2)	546 (1)	637 (1)
18	620 (1)	714 (1)	564 (1)	657 (1)
19	588 (4)	554 (3)	— —	666 (1)
20	550 (1)	860 (1)	— —	696 (1)
21	520 (2)	520 (2)	— —	706 (1)
22	490 (1)	649 (1)	— —	— —
23	— —	736 (1)	— —	— —
24	680 (1)	— —	— —	— —
36	930 (1)	980 (1)	— —	— —

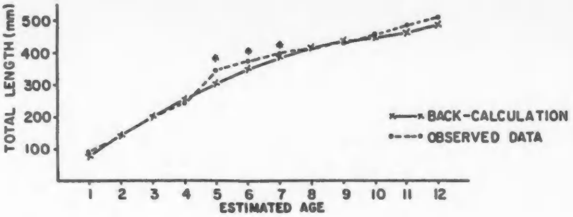

FIGURE 5.—Mean observed and back-calculated lengths for year class of *Netuma barba* (* $P < 0.05$).

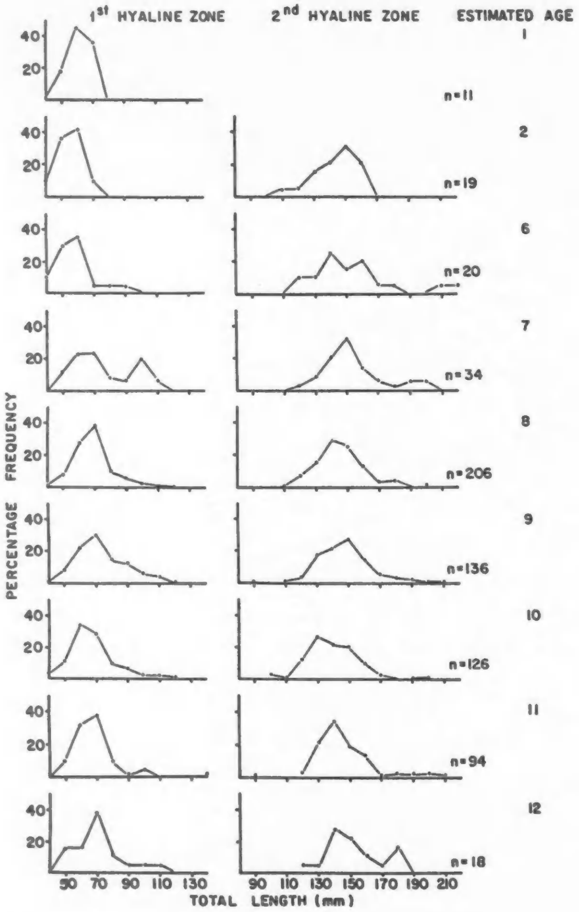

FIGURE 6.—Back-calculated lengths frequencies at first and second hyaline zones for year class of *Netuma barba* (n = number of specimens).

thermore, as the modes for each year class are similar, age determination can be considered consistent.

Validation of Age

Validation of the otolith method for aging *Netuma* barba is supported by the following: 1) one opaque and one hyaline zone is formed annually (Figs. 3, 4); 2) a gradual decrease of length increments with age (Table 1); 3) observed lengths generally agree with back-calculated lengths (Fig. 5); and 4) distribution of back-calculated lengths for previous ages shows similar modes for each year class (Fig. 6).

Length-weight Relationship and Condition Factor

A total of 685 specimens captured during 1980 was used to compute the length-weight relationship for each sex:

Male $Wt = 4.70 \times 10^{-6}\, Lt^{3.14}$ $r = 0.992$ $n = 332$
Female $Wt = 2.19 \times 10^{-6}\, Lt^{3.26}$ $r = 0.952$ $n = 363$
Total $Wt = 4.41 \times 10^{-6}\, Lt^{3.15}$ $r = 0.987$ $n = 685$

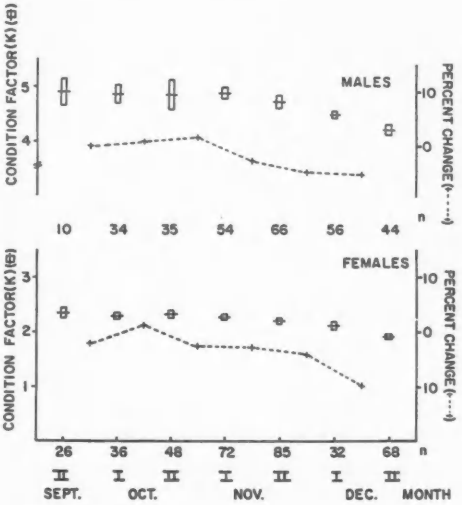

FIGURE 7.—*K* condition factor and percent change for males and females of *Netuma barba* related to time (n = number of specimens; I = first half of the month; II = second half of the month)

The analysis of covariance (Snedecor and Cochran 1970) at $P < 0.05$ level showed significant difference only for the μ value, and for that reason condition factor (*K*) was determined for each sex. There is a decrease of mean *K* values towards the end of the year (Fig. 7). The condition factor for males is always higher probably due to a more intense feeding prior to reproduction. Low *K* values reveal the stress the fish suffers when it is scarcely feeding and fat reserves are being diverted to gonad maturation (Reis in press), thereby causing a cessation of growth. I proposed that *K* values for males will sharply decrease after spawning due to an oral incubation period that lasts 1 to 2 mo and prevents males from feeding (Reis in press).

Calculation of Growth Parameters

Von Bertalanffy growth parameters were estimated by Beverton's (1954) method which presented the smallest residual variance between observed and calculated lengths for year class on the ages that are most affected by gear selectivity (8-12 yr old). For fish populations captured from a certain age onward, the smallest residual variance should be sought for all year classes from age at first capture. For *Netuma barba* the smallest residual variance could not be ascertained by this method because the true length distribution is unknown due to the use of gillnets as fishing gear. Growth equation for age 1 to 12 for both sexes in represented by

$$Lt = 638\,[1 - e^{-0.1287(t+0.195)}].$$

Figure 8 shows both calculated and observed lengths for each year class.

Growth in weight for each sex resulted in

Male $Wt = 2981.89\,[1 - e^{-0.1287(t+0.195)}]^{3.14}$
Female $Wt = 3035.70\,[1 - e^{-0.1287(t+0.195)}]^{3.26}.$

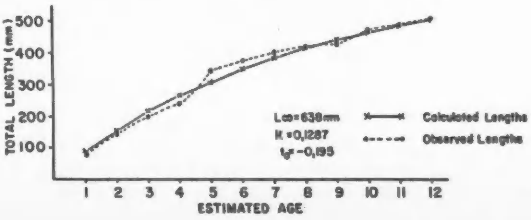

FIGURE 8.—Growth curve of *Netuma barba*.

Maximum Size and Age, Life Span, and Mortality Rate

Netuma barba is a long lived, slow growing species with a low mortality rate. Specimens as long as the theoretical mean length (638 mm) are frequently captured. The largest catfish observed was a 980 mm female 36 yr old. *Netuma barba* life span was estimated to be 23.1 yr and its mortality rate was 0.13. I assumed that the estimate of M (natural mortality) is accurate, since *Netuma barba* reveals a long life span, a capacity to avoid predation through the defense represented by its hard dorsal and pectoral spines and a parent-juvenile care behavior (Reis in press). Pauly (1980) suggested that species with low mortality rates are related to high L_∞ values and to low growth coefficients. These characteristics combined with the fact that *Netuma barba* has a low fecundity (Reis in press) define the species as *K*-strategistic (Gunderson 1980).

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MONITORING THE SEA SURFACE CHLOROPHYLL CONCENTRATION IN THE TROPICAL PACIFIC: CONSEQUENCES OF THE 1982-83 EL NIÑO

YVES DANDONNEAU[1]

ABSTRACT

The sea surface chlorophyll concentration (SSCC) is routinely measured in the tropical Pacific using filtrations made aboard merchant ships that sail from New Caledonia to Japan, North America, Panama, New Zealand, and Australia. About 4,000 measurements are collected every year, allowing a tentative monitoring of SSCC in the Pacific. Heavy smoothing made it possible to map quarterly charts of SSCC which cover the 1982-83 El Niño episode. The usually enriched belt which corresponds to the equatorial upwelling vanished after September 1982, except for a reduced zone east of long. 120°W, where a moderate enrichment persisted throughout the warm event. It recovered after July 1983, spreading westwards to long. 170°E. During the mature phase of El Niño (October 1982-June 1983), an enriched zone appeared in the western Pacific, centered at about lat. 7°N, consistent with a rise of the thermocline in this region. An examination of oceanographic data collected in this region since 1970 shows that nutrients from below the thermocline are consumed by the phytoplankton during each El Niño. This western Pacific enrichment was weakened with time, and the period from April to June 1983 was characterized by low SSCC values over most of the tropical Pacific. Unusually high SSCC values are reported in subtropical zones, during the austral winters of 1982 and 1983 in the southwestern Pacific and during the 1982 autumn in the northeastern Pacific, which may be due to advection of rich water from higher latitudes and to intensified vertical mixing by strong westerly winds, respectively.

El Niño was first observed and experienced in Peru, where it was given its name and became a familiar part of Peruvian life. Although the southern oscillation was identified more than 60 yr ago (Walker 1924), the relation between the El Niño phenomenon and ocean-scale features was only established after the 1957-58 event by Bjerknes (1966). It is now well established that El Niño is simply the most obvious consequence of important oceanographic and meteorological changes in the Pacific Ocean (Donguy and Henin 1976; Quinn et al. 1978; Cane 1983). One would expect biological changes at the same scale. These, however, have only been studied in the eastern Pacific (Walsh 1981; Chelton et al. 1982; Barber and Chavez 1983) where a pronounced decrease in phytoplankton biomass and primary production is observed. Farther west in the equatorial zone, the decrease in primary productivity has been shown only by indirect observations on marine birds (Schreiber and Schreiber 1984) and on abnormal distributions of some fishing grounds in relation to changes of water mass (Donguy et al. 1978; Yamanaka 1984). The difficult problem of monitoring the intensity of primary production on a large scale is usually reserved for satellite-borne sensors. A modest attempt, however, is in progress, as a part of the SURTROPAC program (ORSTOM, Nouméa) based upon chlorophyll samples taken by voluntary observers on ships of opportunity. Each year about 4,000 sea surface chlorophyll concentrations (SSCC) are collected in this way, distributed along maritime lanes from the Tasman Sea to Panama, North America, or Japan. These data cover the tropical Pacific from lat. 30°S to 30°N, and from long. 140°E to 80°W. There are large gaps both in space, between the main lanes, and in time, between consecutive crossings. But, on a quarterly basis, the SSCC data are numerous enough to allow a crude view of the whole tropical Pacific Ocean, with the advantage of using a single methodology. The consequences of the 1982-83 El Niño can thus be examined, and most of the attention will be directed towards the central and western Pacific, where present knowledge is very incomplete.

METHODS

Chlorophyll Measurements

SSCC measurements are made according to a nonextractive method (Dandonneau 1982). Twenty milli-

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[1] Groupe SURTROPAC, Centre ORSTOM, B.P. A5, Nouméa, New Caledonia.

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liters of seawater are filtered on 13 mm HAWP Millipore filters, using a syringe and Swinnex type filtering cartridges. The filters are then stored in a dark place at ambient temperature. When the observing ship reaches Nouméa, the filters are taken to the laboratory for fluorescence measurements. A 3-wk minimum time lag is needed between filtration and measurement, after which degradation processes lead to stable fluorescent chlorophyll by-products on the filters. The fluorescence (Ff) of the filters is then measured without extraction, using a specially adapted sample holder.

The measurement error e is proportional to the chlorophyll concentration C and can be expressed as $e = |\text{SSCC-}C|/C$ where SSCC is measured by the non-extractive method while C is obtained by a more conventional technique (Holm-Hansen et al. 1965). Ninety-five percent of e values are <0.6 (Dandonneau 1982, and confirmed by later tests). This value is probably an overestimate of e since it results both from the error on SSCC and from the unknown error on C. Different phytoplankton populations can also result in different fluorescence to chlorophyll ratios for the dry filters. This ratio has shown no significant change between winter and summer conditions around New Caledonia where a mixed regime alternates with a stratified one (Dandonneau and Gohin 1984). The risk of a variation of the ratio in other environments has not been examined, and must be kept in mind. The few SSCC data points at latitudes higher than 30° were not taken into account for this reason.

Calibrations

SSCC is estimated using $\text{SSCC} = k\,Ff$ where k is a calibration coefficient that must be corrected from time to time. Twenty milliliters from a seawater sample are filtered giving a fluorescence Ff_0 after 21 d of storage. A larger volume V from the same sample is filtered on a glass fiber filter, ground, and extracted by a volume v of 90% acetone. The fluorescence of the extract is Fe_0. Knowing the fluorescence to chlorophyll ratio of the fluorometer, R_0, determined from a known solution of pure chlorophyll a, we can estimate the following chlorophyll concentration of the seawater sample:

$$C_0 = (Fe_0 \times v)/(R_0 \times V);$$

we obtain then $k_0 = Ff_0/C_0$.

k_0 is sensitive to detrital material in turbid coastal waters, so these main calibrations are made during offshore oceanographic cruises. As such opportunities are infrequent, secondary calibrations are made more frequently with known solutions of pure chlorophyll a, giving R_i instead of R_0. We then assume that $k_i = k_0 \times R_i/R_0$. This procedure does not consider correction for chlorophylls b and c, nor does it consider correction for phaeopigments, which has recently proven to be uncertain when the fluorometer is fitted with a commonly supplied blue excitation lamp (Baker et al. 1983). Although the SSCC data presented in this work are expressed in milligrams of chlorophyll a, they should be considered only as indices of phytoplankton abundance.

Data Rejection

The crew members who take the seawater samples and make the filtrations are voluntary observers. Errors may occur which are difficult to detect because, unlike temperature or salinity, 1) any SSCC value in the interval 0-1 $\text{mg}\cdot\text{m}^{-3}$, which covers almost the whole data set, is a possible one anywhere in the tropical Pacific, and 2) the autocorrelation of SSCC decreases very quickly with time or space, so that surrounding data cannot help in error detection. Therefore, all the data are accepted, unless the filter exhibits an obvious fault (i.e., breaking, stain, extraneous material). Occasionally, all the data from a ship's voyage were evidently too high, by a factor 3 or 5. Contamination by a polluted sampling bucket was the cause, and the data from the entire voyage were rejected.

Other possible errors are more insidious, such as insufficient care in keeping the filters out of light, or using an oxidized sampling bucket. These errors result in slightly lowered values, but there is no way to correct them and, in most cases, no way to even detect these biases. Such data are entered in the data bank. As a resulting constraint, any estimate from this SSCC data set must be developed from many data, in order to minimize the effect of a few possibly biased values.

Mapping Techniques

In a previous work (Dandonneau and Gohin 1984) the principles of objective analysis were applied to compute best estimates of SSCC at a given place and time in the southwestern tropical Pacific. The studied area in the current study is much larger and more complex, and the density of data is not high enough to allow good estimates of the statistics of the field. Hence, the use of an objective analysis of the SSCC data has been excluded. The SSCC mapped here on Figure 1 have been estimated using

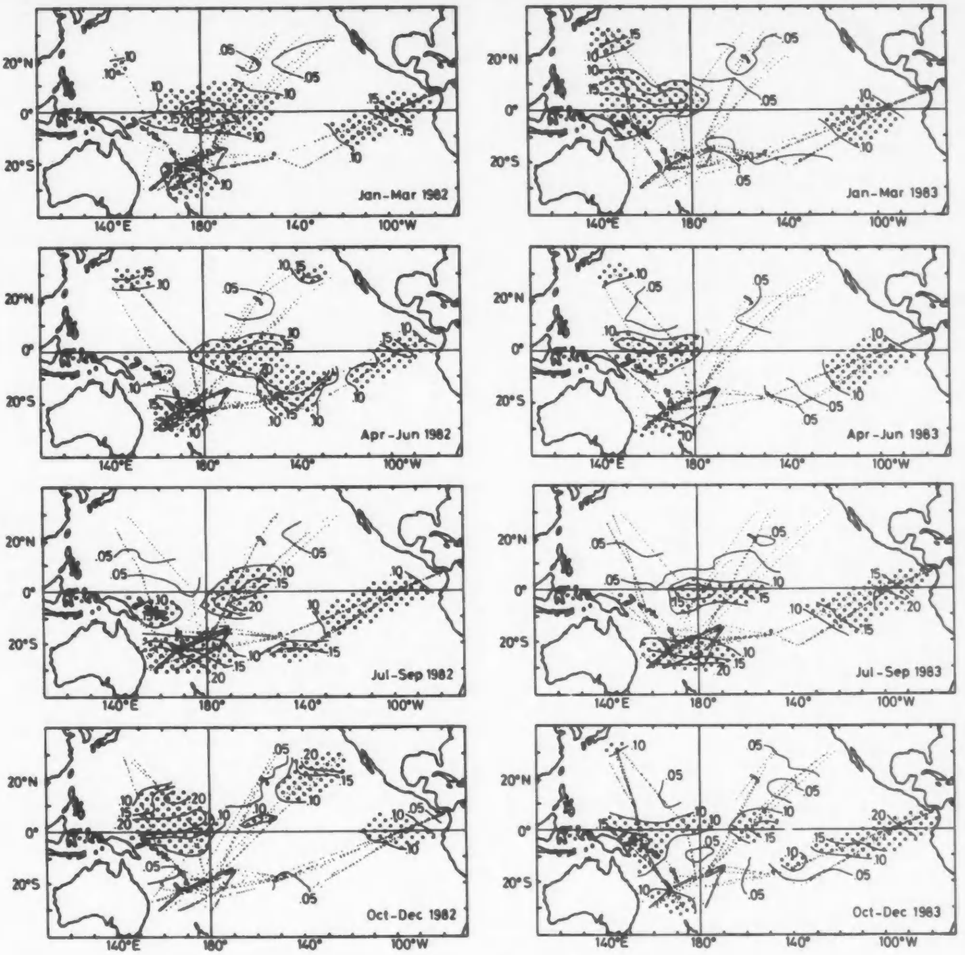

FIGURE 1.—Quarterly charts of SSCC (sea surface chlorophyll concentrations) in the tropical Pacific from January 1, 1982 to December 31, 1983. Areas where SSCC is >0.10 $mg \cdot m^{-3}$ are shaded with large dots. Smaller dots represent the data points.

$$\tilde{t}_j = \sum_{i=1}^{n_j} p_{ij} t_i / \sum_{i=1}^{n_j} p_{ij}$$

where $\tilde{t}_j$ is the SSCC estimate at longitude x_j and latitude y_j, and p_{ij} is the weight given to observation t_i for the estimation $\tilde{t}_j$. p_{ij} is given by

$$p_{ij} = [R^2 + (x_i - x_j)^2 + a^2\,(y_i - y_j)^2]^{-1}$$

where a accounts for anisotropy of the SSCC variations in space. We used $a = 2$, so that observations at a distance Δy in latitude are given the same weight as observations at a distance $\Delta x = 2\Delta y$ in longitude. p_{ij} was set to zero when $(x_i - x_j)^2 + a^2$ $(y_i - y_j)^2$ was >160, so that the observations were considered as "non useful" when outside an ellipse centered at (x_j, y_j) with a principal axis equal to about 25° longitude, and a small axis equal to about 13° latitude. In order to avoid hazardous estimates at the margin of the contoured area, t_j has not been estimated when n_j (the number of useful observations) was <12.

$R = 0$ would give an infinite weight to an observation k available at $x_k = x_j$ and $y_k = y_j$. We would then obtain $t_j = t_k$ regardless of the other observations. This is acceptable only if the instrumental and sampling errors on t_k were null, which is not the case. Thus, R accounts for the errors on the observations. We choose $R^2 = 25$, which, together with $\alpha = 2$ and $p_{ij} > (25 + 160)^{-1}$, performed an efficient smoothing and preserved the large-scale information.

RESULTS

The sequence of quarterly mean SSCC for 1982 and 1983 is presented in Figure 1, together with the positions of the data. The western part, north of lat. 20°N, is poorly sampled. The data range between 0.05 and 0.20 $\text{mg}\cdot\text{m}^{-3}$. The highest values are found during the northern spring of 1982, and the northern winter of 1983. The 1982 winter, and the spring and fall of 1983 exhibit a few values >0.10 $\text{mg}\cdot\text{m}^{-3}$. The 1982 winter and fall show low SSCC, like the summer of both years, below 0.10 $\text{mg}\cdot\text{m}^{-3}$.

The eastern part, north of lat. 10°N, has generally low SSCC values, often below 0.05 $\text{mg}\cdot\text{m}^{-3}$. Exceptions are the spring of 1982 at the extreme north, and, mainly, the fall of 1982 during which the mean values exceeded 0.20 $\text{mg}\cdot\text{m}^{-3}$ off California.

Low SSCC values are observed in the western part between the Equator and lat. 20°N until the summer of 1982. They are abruptly replaced at the end of 1982 by high values which persist until March 1983. Later, low values, generally below 0.05 $\text{mg}\cdot\text{m}^{-3}$, dominate again between lat. 5°N and 20°N, while SSCC >0.10 $\text{mg}\cdot\text{m}^{-3}$ shift back southward to the Equator.

The equatorial zone shows high SSCC in January-March 1982, between America and long. 160°E. Values higher than 0.10 $\text{mg}\cdot\text{m}^{-3}$ spread from lat. 10°N and 10°S in the central Pacific, and to 15°S at 120°W. From April to June 1982, the enriched zone shifts eastwards and southwards. The eastwards shift continues between July and September and is accompanied by a decrease of SSCC in the eastern Pacific, with mean values <0.15 $\text{mg}\cdot\text{m}^{-3}$. From October 1982 to June 1983, a narrow band with SSCC between 0.10 and 0.15 $\text{mg}\cdot\text{m}^{-3}$ in the eastern Pacific is the only remnant of the equatorial enrichment. A normal situation returned after the El Niño, in July-September 1983, with SSCC values >0.15 $\text{mg}\cdot\text{m}^{-3}$ spreading westwards to long. 170°E. In October-December 1983, SSCC >0.10 $\text{mg}\cdot\text{m}^{-3}$ are seen all along the Equator.

South of lat. 20°S, an SSCC increase is observed during the austral winter. The increase started in April-June in 1982, the maximum was reached in July-September, with SSCC >0.20 $\text{mg}\cdot\text{m}^{-3}$ spreading northward to 22°S, and low values were seen again in October-December. The increase during the austral winter of 1983 was of a lesser extent, being well developed only during July-September, with SSCC >0.20 $\text{mg}\cdot\text{m}^{-3}$ limited to the south of 28°S.

The intermediate zone, from lat. 10°S to 20°S, between the equatorial upwelling and higher latitudes where a winter increase is observed, generally has low chlorophyll concentrations, below 0.10 $\text{mg}\cdot\text{m}^{-3}$. The lowest concentrations are seen in austral summer, from October 1982 to June 1983, and in October-December 1983. The highest concentrations are associated with a strengthening of the equatorial upwelling (around long. 140°W in April-June 1982; westwards spreading of richer waters from the eastern Pacific in July-September 1982 and 1983).

When looking at the whole series of maps, the most striking feature is the reduction of the equatorial upwelling enriched area after the onset of El Niño. The most pronounced stage was in April-June 1983, with poor waters over most of the tropical Pacific. On the contrary, a zone centered at lat. 10°N, west of the dateline, which is usually occupied by chlorophyll-poor waters, had higher SSCC during the 1982-83 El Niño.

DISCUSSION

Equatorial Upwelling

The collapse of the equatorial upwelling after the onset of El Niño, when westerlies have replaced the trade winds at the Equator, consistently results in a decrease in SSCC. This decrease has already been documented for the eastern Pacific in the Galapagos Islands region by Feldman et al. (1984) using sea color satellite images. It corresponds to a decrease in primary production of the whole photic layer (Barber and Chavez 1983). The data presented here show that the equatorial zone was impoverished westwards to nearly 180°. This is in agreement with the reproductive failure and disappearance of seabird communities at Christmas Atoll (lat. 2°N, long. 157°W) in November 1982; Schreiber and Schreiber (1984) attributed these events to the establishment of an oligotrophic oceanic ecosystem instead of a productive one. Successful reproduction started again for some birds species in June 1983, and hatching occurred in July-September 1983, when SSCC higher than 0.15 $mg \cdot m^{-3}$ reappeared at the Equator (Fig.1).

Western Pacific Around Lat. 7°N.

Under normal conditions (see Figure 1: January to March 1982, July to December 1983) the equatorial upwelling also drives a chlorophyll-rich zone west of 180°. This does not appear on the map of Koblentz-Mishke et al. (1970) on the primary production in the world ocean, but is described as an episodic feature by Oudot and Wauthy (1976). The area with SSCC >0.15 $mg \cdot m^{-3}$ which appears north of the Equator, centered at about 7°N from October 1982 to March 1983 (Fig. 1) has nothing to do with the equatorial upwelling. Based on approximately 100 SSCC data points obtained by three different merchant ships, this chlorophyll-rich area can hardly be thought to result from measurement errors. It rather may be related to the eastward draining of warm water from the western tropical Pacific and consequent thinning of the surface mixed layer and drop of the sea level (Wyrtki 1985). A simultaneous cooling of the sea surface by 1°C occurred in this region during El Niño, which can be explained by advection of cooler water, and also by other potentially important processes which are more difficult to quantify (Meyers and Donguy 1984). The observed SSCC increase supports the hypothesis that vertical mixing of cooler nutrient-rich deep water might be one of these processes. Even if vertical mixing is unlikely, the 50 m rise of the thermocline which has been observed at lat. 7°N between January 1982 and January 1983 (Meyers and Donguy 1984) allows more light to penetrate to the deep chlorophyll maximum. This hypothesis is supported by the shift which occurred between January 1982 and January 1983 in the nitrate-temperature relationship (Fig. 2; data collected by the Japan Meteorological Agency along long. 137°E aboard RV *Ryofu Maru*; Anonymous 1972-84). The nitrate concentration at a given temperature (which we assume to represent a given water mass) dropped by about 2 $\mu moles \cdot L^{-1}$. Shifts in the nitrate-temperature relationship provide information on the consumption of nitrate by the phyto-

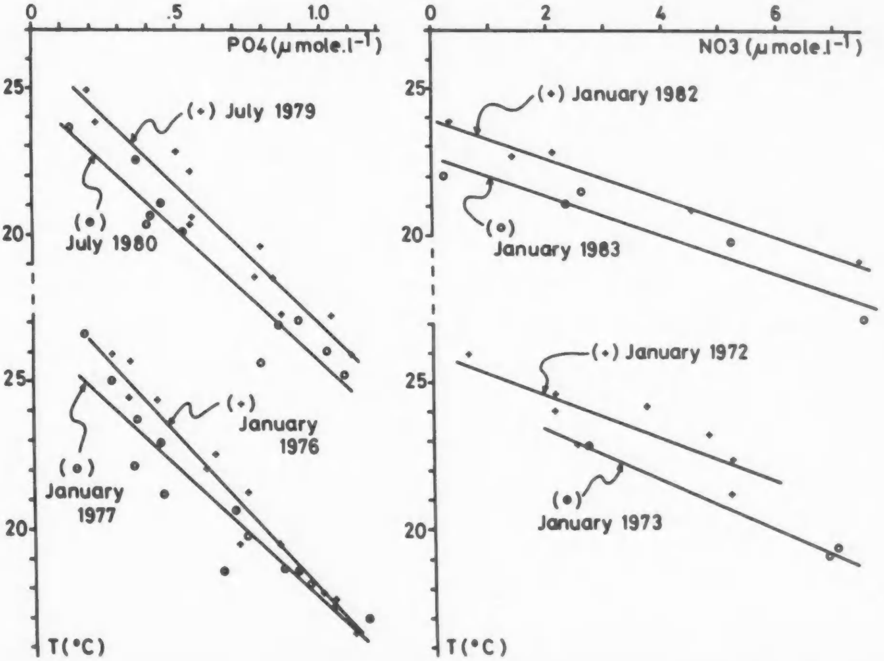

FIGURE 2.—Nutrient-temperature relationships between lat. 6°N and 9°N. Crosses: observations before an El Niño; open circles: observations after an El Niño. (Data from the RV *Ryofu Maru* cruises at long. 137°E, Anonymous 1972 to 1984).

plankton (Voituriez and Herbland 1984). We can then suggest that new nitrates have been assimilated during El Niño in the western Pacific at lat. 6-9°N. The 2 μmoles$\cdot$L^{-1} drop in nitrate concentration is observed in the interval 17°-22°C, corresponding to a 35 m thick water layer (Anonymous 1972-84), so that the amount of new nitrates used by photosynthesis is 70 μmoles$\cdot$m^{-2}, or 980 mg$\cdot$m^{-2}. If $C/N = 9.01$ and $C/Chl = 114$ in surface waters of the oligotrophic central North Pacific (Sharp et al. 1980), this amount of nitrogen corresponds to 77 mg Chl a$\cdot$m^{-2}. It represents an important supply in an ecosystem where the chlorophyll concentration is usually low.

Figure 3 shows the variations of integrated chlorophyll (0-200 m) between lat. 6°N and 9°N at long. 137°E, obtained from the *Ryofu Maru* data (Anonymous 1972-84). Values during the 1982-83 El Niño are similar to those since July 1981, i.e., below 50 mg$\cdot$m^{-2}. SSCC from the same data set also shows low values during the 1982-83 El Niño, conflicting with the results mapped on Figure 1. Recent El Niño events in 1972 and 1976 resulted in a drop of the sea level in the western Pacific (Meyers 1982). Low sea level was also recorded during an El Niño like event in the western Pacific in 1979-80 (Donguy and Dessier 1983). These low sea level episodes during which the thermocline is shallow (Wyrtki 1978), yet do not correspond to high SSCC or high integrated chlorophyll values in the *Ryofu Maru* results (Fig. 3). It seems however that the nutricline depth is shallower during these four episodes (Fig. 3). All of them are moreover characterized by a shift in the nutrient-temperature relationship (Fig. 2) indicating a consumption of new nutrients. We are dealing with an SSCC enrichment in the northwestern tropical Pacific which persists for several months (October 1982-March 1983) and is consistent with an input of new nutrients from below, but which does not appear in the chlorophyll concentrations measured every 6 mo on the *Ryofu Maru*. Both data sources have weaknesses. The SSCC monitoring does not measure what occurs below the surface. A significant correlation exists between SSCC and integrated chlorophyll on broad data sets (Lorenzen 1970; Platt and Herman 1983), but oligotrophic ecosystems often show no relationship or, sometimes, inverse relationships (Hayward and Venrick 1982). The *Ryofu Maru* data at 137°E between 6°N and 9°N allow a look at this problem (Fig. 4): the correlation between SSCC and integrated chlorophyll is significant at the 1% level. The value $r = 0.52$ obtained with individual stations increases to $r = 0.70$ when enlarging the spatial scale (i.e., taking mean values between 6°N and 9°N instead of individual stations); a further improvement would probably be obtained by enlarging the time scale, but appropriate time series do not exist

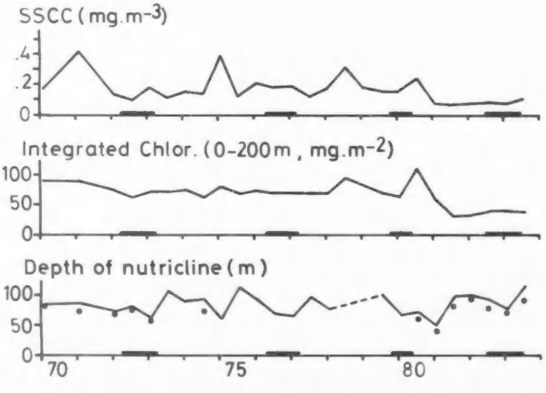

FIGURE 3.—Long-term evolution of lat. 6°N-9°N averaged parameters related to the primary production (data from the RV *Ryofu Maru* cruises at long. 137°E, Anonymous 1972 to 1984). Upper and middle panels: the chlorophyll concentrations primarily expressed in active chlorophyll a and pheophytin have been converted into chlorophyll a equivalents (Dandonneau 1979). Lower panel: the continuous line joins the depth of $PO_4 = 0.35$ μmole$\cdot$L^{-1}; open circles represent the depths of $NO_3 = 1$ μmole$\cdot$L^{-1}. Thickened marks on the horizontal axis indicate the low sea level episodes in the western tropical Pacific.

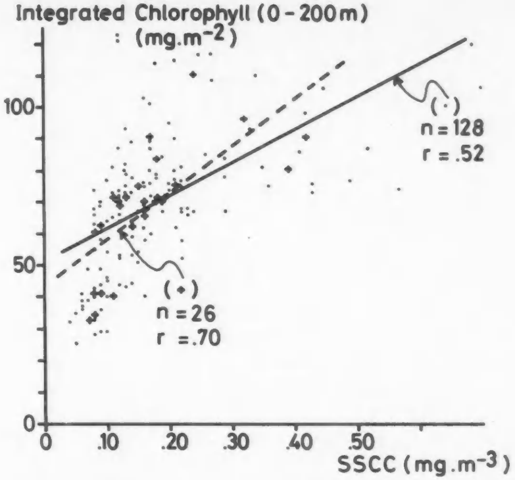

FIGURE 4.—Integrated chlorophyll (0-200 m)/SSCC relationship between lat. 6°N and 9°N (data from the RV *Ryofu Maru* cruises at long. 137°E, Anonymous 1972 to 1984). Points and continuous line: individual stations. Crosses and dashed line: averaged values for each cruise.

in this region. We can thus conclude that SSCC is a reasonable index of the chlorophyll content in the photic layer. The weakness of the *Ryofu Maru* data series is that only 4-6 stations within 3 d are available for each El Niño episode. This sampling pattern can describe the vertical structure of the ocean, but it is not helpful in large-scale studies based on chlorophyll, in which the signal to noise ratio is very low (Dandonneau and Gohin 1984).

Subtropical Zones

At the start of the 1982-83 El Niño (and a possible cause of it?) strong southerly winds were recorded east of Australia in June and July 1982 (Harrison and Cane 1984). In the Coral and Tasman Seas, a chlorophyll enrichment occurs in austral winter between 22°S and higher latitudes (Dandonneau and Gohin 1984). This chlorophyll enrichment can be seen in austral autumn and winter of 1982 (Fig. 1), while it only appears in winter in 1983. Moreover, SSCC higher than 0.15 $\mathrm{mg \cdot m^{-3}}$ spread northward to lat. 20°S in July-September 1982 around long. 160°E, but only to 24°S in July-September 1983 at the same longitude. The long and intense SSCC winter increase in this area in 1982 may be the result of advection of richer water from the south after the strong wind anomaly. In the Northern Hemisphere, a zone with high SSCC values is observed off North America during the fall of 1982 (Fig. 1); this feature is especially noteworthy since most regions of the Pacific (even those from the same merchant ship voyage) show low SSCC values. Like other El Niños, the 1982-83 one resulted in temperatures and sea levels higher than normal along the California coast, and strong westerly winds at about 30°N. One would not expect increased chlorophyll concentrations with higher temperatures, and according to Chelton et al. (1982), El Niño episodes are likely to diminish advection of water from the north which generates a higher biomass. However, our data points corresponding to the enriched zone were far offshore (Fig. 1) and the thermal anomaly there did not greatly differ from zero. The high SSCC values off North America during the fall of 1982 might then be related to the severe wind conditions which prevailed during this time, and probably induced vertical mixing of deep nutrients.

A few more features which appear on Figure 1 would be worthy of discussion, but conclusion is hindered by the lack of accordance with a poorly known field of oceanic properties and by the risk of sampling or instrumental errors in SSCC measurements. For instance the shape of the area with SSCC >0.15 $\mathrm{mg \cdot m^{-3}}$ centered slightly south of the Equator at 165°W in July-September 1982 (Fig. 1), while the upwelling was collapsing, is surprisingly similar to the shape of the maximum of cloudiness in September 1982, derived from satellite measurements of outgoing long wave radiation (Gill and Rasmusson 1983). Similarity might be causal, i.e., high SSCC values might result from a response of the phytoplankton to attenuation of light by the clouds, or from enhanced phytoplankton growth caused by precipitation of dust and aerosols by the rain (Menzel and Spaeth 1962). It may also result, at least partly, from sampling artifacts.

The major features shown by this SSCC monitoring experiment are in agreement with the large-scale processes that affect the tropical Pacific during El Niño episodes. The collapse of the equatorial upwelling in October 1982 resulted in a nearly complete disappearance of the chlorophyll-rich area which is usually located across the Equator. A moderate enrichment persisted, however, east of long. 120°W. In the northwestern tropical Pacific, the eastward drift of the warmwater pool was followed by conditions which stimulated photosynthesis: a shallower thermocline, and more light penetrating to the nutrients gave rise to unusually high chlorophyll concentrations west of 180° from October 1982 to March 1983. In April-June 1983, the equatorial upwelling in the eastern Pacific was still reduced by the El Niño conditions, and the enrichment in the northwestern tropical Pacific was less intense; during this period, low chlorophyll concentrations prevailed over most of the tropical Pacific.

ACKNOWLEDGMENTS

I would like to thank Henri Walico for the thousands of chlorophyll measurements which are the basis of the present work. I am indebted to the captains and crews of the merchant ships who call at Nouméa for kindly and carefully sampling and filtering at sea.

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ANATOMICAL TRAUMA TO SPONGE-CORAL REEF FISHES CAPTURED BY TRAWLING AND ANGLING

S. Gordon Rogers,[1] Hiram T. Langston,[2] and
Timothy E. Targett[3]

ABSTRACT

External signs of trauma were examined in 15 sponge-coral reef fish species captured while trawling and angling at 37 m depth. Internal evidence of trauma was noted for all species and quantified for a sample of angling-caught black sea bass, *Centropristis striata*. Distinct differences were noted in the types and frequencies of trauma experienced among species, and between gear types within species. Black sea bass; red snappers, *Lutjanus campechanus*; short bigeyes, *Pristigenys alta*; and *Mycteroperca* groupers exhibited high frequencies of oral protrusions. Planehead filefish, *Monacanthus hispidus*; orange filefish, *Aleuterus schoepfi*; and blue angelfish, *Holacanthus bermudensis*, were particularly prone to cloacal protrusions. External signs of trauma were few in vermilion snappers, *Rhomboplites aurorubens*; porgies (*Stemotomus chrysops*, *Calamus leucosteus*, and *Pagrus pagrus*); tomtates, *Haemulon aurolineatum*; and two trawl-caught serranids (*Centropristis ocyurus* and *Diplectrum formosum*). Angling produced oral protrusions in black sea bass more frequently than trawling. Trawl-caught red snappers had a higher stomach eversion frequency when brought to the surface more quickly. Angling-caught black sea bass experienced high frequencies of tissue emphysema and swim-bladder rupture. These results should be considered in studies of feeding biology, released-fish survivorship, and fishery management.

Anatomical trauma experienced by fishes during capture is interesting from several standpoints. Mortality of individuals caused by stress, tissue damage, organ displacement, and resulting aberrant behavior has been recognized primarily for its effects on the survival of released fish in mark-and-recapture studies (Ricker 1949; Parker et al. 1959, 1963; Gotshall 1964; Beamish 1966; Moe 1966; Laird and Stott 1978; Pawson and Lockwood 1980; Fable 1980; Grimes et al. 1983). Mortality of fishes released by fishermen is an important consideration for stock assessment and management (Black 1958; Pawson and Lockwood 1980; Matheson and Huntsman 1984). Recent management plans for the U.S. Gulf and South Atlantic snapper-grouper fisheries (GOMFMC 1981; SAFMC 1983a, b) recommended implementation of minimum sizes for several species. The sizes in the South Atlantic were determined from yield-per-recruit (YPR) models incorporating assumed survival rates for undersized, released fishes (SAFMC 1983a). Size regulations were predicted on survivorship of ≥60%. Gulf YPR models did not incorporate survival rates, effectively assuming 100% survival.

Other workers have indicated difficulty in obtaining specimens of snapper-grouper species for quantitative analyses of feeding biology from depths which caused stomach eversion and loss of gut contents (Stearns 1884; Adams and Kendall 1891; Camber 1955; Mosely 1966; Moe 1969; Bradley and Bryan 1975; Link 1980; Ross 1982). This is of particular concern for studies comparing food habits across depth zones (Moseley 1966). Differences between fish species captured by identical gear at similar depths and differences within species between gear types introduce additional variation. This study addresses the types and frequencies of anatomical trauma experienced by sponge-coral reef fishes captured by angling and trawling at a single depth. These data are discussed in relation to trophic studies, future studies of trauma during capture, survival following release, and management of snapper-grouper fisheries.

METHODS

Fishes were caught by angling and trawling at a low-relief (<1 m) sponge-coral reef 37 m deep on the continental shelf 84 km east of Sapelo Island, GA

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[1] Skidaway Institute of Oceanography, University System of Georgia, POB 13687, Savannah, GA 31416; present address: Coastal Resources Division, Georgia Department of Natural Resources, 1200 Glynn Avenue, Brunswick, GA 31523.

[2] Skidaway Institute of Oceanography, University System of Georgia, POB 13687, Savannah, GA 31416.

[3] Skidaway Institute of Oceanography, University System of Georgia, POB 13687, Savannah, GA 31416; present address: University of Delaware, College of Marine Studies, Lewes, DE 19958.

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(lat. 31°26′N, long. 80°20′W; central South Atlantic Bight). Angling gear was standard hand-operated boat rods rigged with double-hooked terminal tackle and baited with squid. Hook sizes were 3/0 to 5/0. Fishes were brought to the surface as quickly as possible (about 1 m/s; somewhat slower for large snappers and groupers). Trawling was conducted from two vessels, each rigged for stern trawling but with some differences in gear and handling.

The trawl gear on the RV *Georgia Bulldog* was a 25 m, 4-seam high-rise roller trawl with tongue. Meshes were (stretched) 20 cm in the wings and tongue, 10 cm in the belly and bag (2 cm liner), and 7.5 cm in an extension. Cables connecting the trawl and doors produced a sweep of 31.1 m; the rise on the tongue was 6.1 m (J. B. Rivers[4]). The rig had a vertical haulback rate of 0.12-0.15 m/s.

The trawl gear on the RV *Blue Fin* was a modified No. 36 Yankee flat roller trawl. Meshes were (stretched) 5 cm in the wings and belly and 3.5 cm in the bag (2 cm liner). The total sweep was 22.1 m and the rise at the center of the headrope was 3.7 m (Rivers fn. 4). The rig had a vertical haulback rate of 0.1 m/s. Gear handling was otherwise identical.

Tows were 20 min long. The fish catch was sorted to species and the alimentary tracts samples removed; or samples were placed in 20 L buckets with ice-seawater mixture, frozen on board, and processed in the laboratory. Data on anatomical trauma were recorded during dissections. An angling catch of 34 black sea bass, *Centropristis striata*, was put on ice and dissected 2 days later for examination of internal trauma. No samples were subjected to the bin-type icing procedures common on commercial snapper-grouper vessels. Fishes were collected from July through December in 1983 and in September 1984.

External evidence of trauma consisted of several types of protrusion of the gastrointestinal tract. These were classified as

1) Oral eversion - stomach everted into the pharynx and often present in the mouth, pulling the pyloric area and the intestine with it.
2) Cloacal protrusion - intestine protruded from the cloacal area. Initially such protrusions were not classified further; however, detailed dissections showed that they were either
    a) Herniations - disruptions of the body wall in the pericloacal area through which the gut protruded or
    b) Intussusceptions - actual eversion of the terminal portion of the intestine through its own lumen.
3) Branchial protrusions - portions of the gut protruded through the branchial opening.

Results are expressed as occurrences and percentage frequencies. Frequencies of herniations and intussusceptions were calculated by dividing the observed number in a class by the total number of classified cloacal protrusions, then multiplying the result by the total proportion of cloacal protrusions. Example (from Table 1): planehead filefish herniations, $(99/(99+22))(160/440) = 0.30$.

Internal evidence of trauma included 1) the presence of gas in the tissues (tissue emphysema) and 2) rupture of the swim bladder. Although notes on both phenomena were kept for all fish species, their frequencies were enumerated only for the 34 carefully examined, angling-caught black sea bass.

Among-species and between-gear comparisons of trauma were performed by using Pearson's test for goodness of fit (yielding a χ^2 value). The null hypotheses were specified as homogenous (equal) proportions of specimens exhibiting a particular symptom, based on the overall proportion of fish with the symptom across species or gears (significant departures were $P < 0.05$).

RESULTS

Dissection records of 1928 trawl-caught and 235 angling-caught fishes of 15 species were collated for external evidence of trauma (Table 1). Seven species were not caught with angling gear. Scamp, *Mycteroperca phenax*, and gag, *M. microlepis*, were combined to form a *Mycteroperca* grouper category due to low numbers collected.

Trawl-caught red snappers, *Lutjanus campechanus*; *Mycteroperca* groupers; short bigeyes, *Pristigenys alta*; planehead filefish, *Monacathus hispidus*; orange filefish, *Aleuterus schoepfi*; and blue angelfish, *Holacanthus bermudensis*, experienced frequent gut displacements (Table 1). These were oral eversions in red snappers, short bigeyes, and *Mycteroperca* groupers; cloacal protrusions in orange filefish and blue angelfish; and all three categories (including branchial protrusion) in planehead filefish. Alimentary tract displacements were minimal in trawl-caught black sea bass; bank sea bass, *Centropristis ocyurus*; sand perch, *Diplectrum formosum*;

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[4] J. B. Rivers, Marine Fisheries Specialist, University of Georgia Fisheries Extension Station, POB Z, Brunswick, GA 31523, pers. commun. October 1984.

TABLE 1.—Numbers and percentage frequencies (in parentheses; a = 1%) of alimentary tract displacements in sponge-coral reef fishes collected by trawling (T) and angling (A) in 37 m depth. Dashes (—) indicate no data. Within cloacal protrusions, H = herniations, I = intussusceptions, U = unclassified, and TC = total cloacal. *N* = number of specimens examined.

Species		Oral eversions	Cloacal protrusions				Branchial protrusions	Total displacements	*N*
			H	I	U	TC			
black sea bass	T	4(2)	0	0	0	0	0	4(2)	200
Centropristis striata	A	45(27)	0	0	0	0	0	45(27)	169
red snapper	T	26(55)	0	0	0	0	0	26(55)	47
Lutjanus campechanus	A	1(50)	0	0	0	0	0	1(50)	2
bank sea bass	T	0	0	0	0	0	0	0	39
Centropristis ocyurus	A	1(33)	0	0	0	0	0	1(33)	3
short bigeye	T	8(22)	0	0	0	0	0	8(22)	37
Pristigenys alta	A	—	—	—	—	—	—	—	0
sand perch	T	0	0	0	0	0	0	0	19
Diplectrum formosum	A	2(18)	0	0	0	0	0	0	11
Mycteroperca groupers	T	5(29)	0	0	0	0	0	5(29)	17
	A	0	0	0	0	0	0	0	1
planehead filefish	T	3(1)	99(30)	22(7)	39	160(36)	14(3)	177(40)	440
Monacanthus hispidus	A	—	—	—	—	—	—	—	0
orange filefish	T	0	1(4)	4(17)	7	12(21)	0	12(21)	58
Aleuterus schoepfi	A	—	—	—	—	—	—	—	0
blue angelfish	T	0	4(30)	1(8)	4	9(38)	0	9(38)	24
Holacanthus bermudensis	A	—	—	—	—	—	—	—	0
vermilion snapper	T	0	0	0	0	0	0	0	339
Rhomboplites aurorubens	A	0	0	0	1	1(4)	0	1(4)	28
whitebone porgy	T	0	1(3)	1(3)	0	2(6)	0	2(6)	33
Calamus leucosteus	A	—	—	—	—	—	—	—	0
scup	T	0	1(1)	0	2	3(1)	0	3(1)	286
Stenotomus chrysops	A	—	—	—	—	—	—	—	0
tomtate	T	0	0	0	2	2(a)	0	2(a)	372
Haemulon aurolineatum	A	—	—	—	—	—	—	—	0
red porgy	T	0	0	1(6)	0	1(6)	1(6)	2(12)	17
Pagrus pagrus	A	0	0	0	0	0	0	0	21

tomtate, *Haemulon aurolineatum*; scup[5], *Stenotomus chrysops*; whitebone porgies, *Calamus leucosteur*; red porgies, *Pagrus pagrus*; and vermilion snappers, *Rhomboplites aurorubens*.

Angling-caught black sea bass had high frequencies of oral eversion. Angling-caught red porgies and vermilion snappers exhibited few or no protrusions. Angling data for all other species are too sparse to estimate protrusion frequencies.

There was a significant lack of homogeneity in the frequencies of oral eversions between species within trawl (χ^2 = 695, df = 13, $P \ll 0.01$) and angling-caught (χ^2 = 14.2, df = 6, $P < 0.05$) samples. The trawling value resulted from high frequencies for red snapper, *Mycteroperca* groupers, and short bigeye; these three categories accounted for 95% of the χ^2 statistic. Among angling-caught fishes, a high value for black sea bass and low values for red porgy and vermilion snapper accounted for 91% of the χ^2 statistic.

The high frequencies of cloacal protrusions in trawl-caught planehead filefish, orange filefish, and blue angelfish (21-38%) and low values in all other species (<7%) produced a highly significant departure from homogeneity (χ^2 = 470, df = 13, $P \ll$ 0.001). Seven of the 15 fish species did not display the symptom (Table 1). Only one of the angling-caught specimens (a vermilion snapper) experienced cloacal protrusion. Of those cloacal protrusions classified for blue angelfish and the two filefish species, all herniations (Table 1) had fecal material in the protruded gut portion.

Only planehead filefish experienced branchial protrusions. Tomtate, vermilion snapper, scup, red porgy, and whitebone porgy were notably free of all forms of alimentary tract displacement.

Swim-bladder rupture was noted for all fish species. Tissue emphysema was detected only in black sea bass. Of the 34 black sea bass examined in detail for internal trauma, 33 (97%)

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[5] The taxonomic status of this species is unclear (B. Roumillat, South Carolina Marine Resources Research Institute, POB 12559, Charleston, SC, 29412 pers. commun.) and is properly listed as scup (*Stenotomus chrysops* (Robins et al. 1980; SAFMC 1983a, b)) although several authors have recently used the nomen southern porgy (*S. aculeatus* (Miller and Richards 1980; Wenner 1983; Sedberry and Van Dolah 1984)). Still others have classified South Atlantic-caught *Stenotomus* as longspine porgy (*S. caprinus* (Chester et al. 1984)).

exhibited swim-bladder rupture (1 specimen had 2 points of rupture), and 27 (79%) had tissue emphysema.

Significantly more angling-caught black sea bass had oral protrusions than those caught by trawling (χ^2 = 138, df = 1, $P << 0.001$). For trawl-caught red snappers, significantly more fish caught aboard the *Georgia Bulldog* (26 of 39) had oral eversions than those caught aboard the *Blue Fin* (0 of 8) (χ^2 = 5.34, df = 1, $P < 0.025$). No other comparisons for combinations of symptoms, species, and gear types yielded significant results. However, all oral eversions noted for *Mycteroperca* groupers were produced by *Georgia Bulldog* trawling gear, and those noted for sand perch were produced by angling gear.

DISCUSSION

Differences Due to Species and Gear

Differences between fish species (captured by identical gear) in the type and frequency of gut displacement are likely due to differences in bone structure and relative swim-bladder volume. Except for planehead filefish, which exhibited all forms of external evidence, those species which experienced frequent oral eversions did not present cloacal eversions and vice versa (Table 1; refer also to the analyses of categorized data). In this study the leatherjackets (Balistidae) and angelfishes (Holacanthidae) experienced high frequencies of gut displacements toward the cloacal area. These taxa have a relatively restricted pharyngeal area and the leatherjackets have a bony sternum which further defines a "path of least resistance" toward the cloaca. Other fishes which may be similarly susceptible to cloacal protrusions include other balistids, acanthurids, chaetodontids, and scarids.

Larger mouthed species such as lutjanids (Stearns 1884; Adams and Kendall 1891; Camber 1955; Moseley 1966; Bradley and Bryan 1975; this study), serranids (Moe 1969; Link 1980; Matheson and Huntsman 1984; this study), priacanthids (this study), and scorpaenids (Gotshall 1964) experience oral eversion more frequently than cloacal protrusion. Fishes with medium-sized mouths and "nondirecting" body morphologies (e.g., vermilion snapper, tomtate, and sparids in this study) exhibit neither type of gut protrusion, instead having a general swelling of the body cavity.

The relative volume of the swim bladder varies from 0 to 6% of total body volume in marine fishes (Jones 1957). Although measurements were not made, the patterns of protrusion in this and other studies (above) suggest that species-specific differences in swim-bladder volume result in varying degrees of internal pressure on ascent. This may contribute to differences in gut protrusion and the extent of body cavity swelling.

It is not clear why varying rates of ascent would induce varying frequencies of gut protrusion within a fish species. Differences between fish species in the rates at which gases can be resorbed from the swim bladder likely had little effect on patterns of protrusion. Achievement of equilibrium through resorption requires time on the order of hours (Brown 1939; Jones 1951). This is a longer time-scale than the normal vertical movements of most fishes (Steen 1970) and vertical displacements while trawling and angling. Also, the absolute magnitude of swim-bladder expansion is independent of the rate of ascent and should not be considered a factor. Yet, a pattern is apparent in the higher values for angling versus trawl-caught black sea bass and also for red snappers caught with *Georgia Bulldog* versus *Blue Fin* trawling gear. Mosely (1966) reported higher oral eversion frequencies for red snappers taken by angling versus those taken while trawling at intermediate shelf depths (42-60 m). Bradley and Bryan (1975) also noted for red snappers that angling produced more stomach eversions than trawling, but stated that their data were confounded by differences in the average depths of fishing efforts. Additionally, stomach eversion frequencies for our trawl-caught red snappers (83% taken with "rapid ascent" *Georgia Bulldog* gear) were 7.5-9.5 times higher than those reported in the literature from similar depths (Fig. 1A; Moseley 1966; Bradley and Bryan 1975). It is tempting to attribute these results to differences in vertical haulback rates. The rate of swim-bladder expansion, linked directly to changes in hydrostasis (Steen 1970) and therefore qualitatively more or less "violent", may govern the nature and extent of injuries.

An additional factor contributing potentially to the types and frequencies of gut protrusion is the consistency, amount, and position of prey material in the alimentary tract. Firm material may function as a bonelike directing structure or be what an expanding swim bladder acts upon. It is interesting that all of the herniated intestines in planehead filefish, blue angel fish, and orange filefish contain fecal material. If hydrostatic forces within a fish's body cavity are influenced by gut contents, unequal and variable allocation of sampling effort and catch over a diel feeding cycle could alter estimates of protrusion frequency for a given fish species. The major-

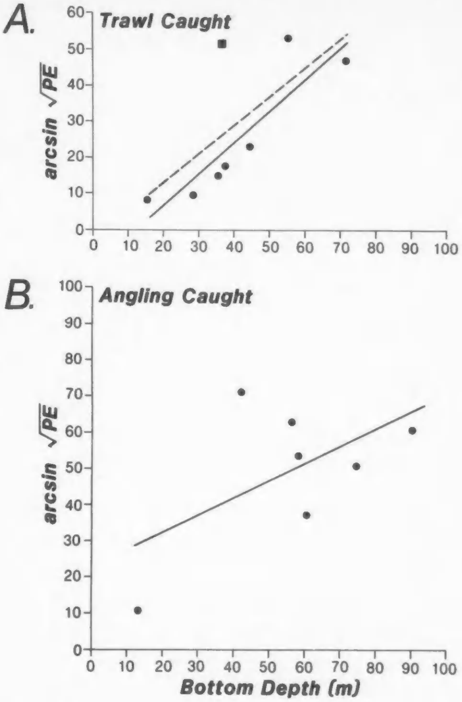

FIGURE 1.—Plots of the proportions of red snappers with everted stomachs (PE) captured by (*A*) trawling and (*B*) angling as a function of bottom depth (data from Camber 1955; Moseley 1966; Bradley and Bryan 1975; except this study). Ordinates were arcsine transformed (Snedecor and Cochran 1980). Abscissas are plotted as actual depths or midpoints of ranges. The dashed line (plot *A*) is the least-squares line including data from this study. The only significant relationship was for trawl-caught fishes from the literature ($r = 0.90$, df = 5, $P < 0.01$).

ity of orange filefish were collected during periods of the day when there was very little material in the alimentary tract, which is likely responsible for herniation/intussesception rates at variance with planehead filefish and blue angelfish values. Sampling of other species was more equitably distributed over the 24-h period.

Considerations for Feeding Studies

Negligible biases in stomach and intestinal contents are expected among trawl-caught black sea bass, bank sea bass, tomtate, the three porgy species, sand perch, and vermilion snapper at depths of 37 m. Angling-caught red porgies and vermilion snappers should be equally free of bias-producing gut displacements at these depths. However, caution is necessary in analyses of stomach contents for trawl-caught red snappers, *Mycteroperca* groupers, short bigeyes, and angling-caught black sea bass from 37 m. Stomach content data for angling-caught red snappers, groupers, bank sea bass, and sand perch should also be interpreted with attention to the likelihood of bias. These considerations have been previously acknowledged for angling-caught black sea bass and bank sea bass (Link 1980), trawl and angling-caught red snappers (Stearns 1884; Adams and Kendall 1891; Camber 1955; Moseley 1966; Bradley and Bryan 1975), angling-caught red groupers, *Epinephelus morio* (Moe 1969), and angling and longline-caught blueline tilefish, *Caulolatilus microps* (Ross 1982), from southeastern U.S. shelf and slope waters. Moseley (1966) and Link (1980) both stated that partial or full stomach eversion renders quantification of consumed prey suspect, particularly with respect to across-depth comparisons (e.g., Godfriaux 1974). Studies of food habits of fishes in the South Atlantic and Gulf of Mexico shelf snapper-grouper complex have either not discussed depth as a diet-determining variable (Camber 1955; Moseley 1966; Moe 1969; Bradley and Bryan 1975; Dixon 1975; Henwood et al. 1978; Ross 1982; Steimle and Ogren 1982) or if depth was considered, dealt with fishes not prone to stomach-eversion bias (Manooch 1977; Grimes 1979; Sedberry 1985).

Species and gear-specific considerations should also be made for analyses of daily feeding chronologies and rations based on stomach content weights. Fishes with partially or completely everted stomachs should be eliminated from the data set. It is clear that trawl-caught specimens of most species are more suited to such analyses than those caught with angling gear. However, some species cannot be efficiently collected with trawling gear at certain times of day, over certain types of bottom, or indeed at all. Extra angling effort (offsetting eversion rates) and well-designed multigear approaches (including traps and longlines) can be used to complete data sets for such fishes.

Displacements of the posterior portion of the alimentary tract can also have significant effects on studies of feeding biology. Trawl-caught planehead filefish, blue angelfish, and orange filefish are subject to such bias. Prey position data used to examine the rate of movement and evacuation of material through the gut (e.g., Klumpp and Nichols 1983) will be affected by both herniations and intussusceptions. During herniation, fecal material is either shifted into the protruded portion of the intestine or the material already present in that segment is isolated from what might otherwise be a continuous column of material. Both potentially produce gaps or "clumping" of intestinal contents. Collection of data affected by intestinal displacements should also incorporate increased sampling so that specimens with herniations or intussusceptions can be eliminated from the data set without a significant loss of information.

Survivorship: Experimental Design and Fishery Management

Our data show that experimental studies of survivorship and the physiological responses of sponge-coral reef fishes following capture and release should stratify their designs by gear. Traps and longlines should be considered in future studies because of the gear-specific vertical haulback rates and other stress factors. Additional considerations are capture depth (Gotshall 1964; Moe 1966, 1969; Moseley 1966; Bradley and Bryan 1975; Grimes et al. 1983), predation on injured and disoriented fishes (Parker et al. 1959, 1963; Randall 1960; Topp 1963; Gotshall 1964; Fable 1980), crowding and abrasion in the gear (Pawson and Lockwood 1980), degree of gut fullness (related to stress from diverted blood supply; Beamish 1966), physiological state related to long-term feeding/activity cycles (Parker et al. 1959), water column temperature structure, currents, and turbidity. Many of the factors covary with depth and fluctuate seasonally.

The anatomical derangements investigated in the present study are severe trauma. Oral and cloacal protrusions would very likely cause high rates of mortality in subsequently released fishes. Obstruction of the gastrointestinal tract would normally be serious and interference with the blood supply to the gastric and intestinal walls would lead to severe circulatory impairment. Gotshall (1964) has shown that returns from tagged blue rockfish, *Sebastes mystinus* requiring stomach replacement and swim-bladder deflation were less than half those from fish requiring only swim-bladder deflation. These fish endured everted stomachs for only a few minutes. Topp (1963) has noted that the everted stomachs of *Lutjanus* snappers are frequently perforated by the fish's teeth. The effects of such injuries on survival require further study.

Expansion of the swim bladder in specimens which do not experience gut protrusions likely induces internal damage undetected by external examination. Aquarists commonly use swim-bladder deflation techniques to increase survivorship of specimens suffering from decompression symptoms (D. Miller[6]). Gotshall (1964) increased tag returns of blue rockfish by deflating expanded swim bladders of specimens collected as deep as 90 m. The technique also reduces the effects of exopthalmia (protruding eyes produced by expansion of gas into the cranial region) on blue rockfish (Gotshall 1964), vermilion snapper, big eye (*Priacanthus arenatus*), and short bigeye (D. Miller fn. 6).

Although tissue emphysema per se may not be lethal, swim-bladder rupture probably is for some species. Jones (1949) reported 90% mortality of 600 perches, *Perca fluviatilis*, with swim bladders ruptured while being raised rapidly from 13.7 m. Topp (1963) speculated that survivorship of sponge-coral reef fishes with ruptured swim bladders is very low. However, R. O. Parker[7] has observed healing of ruptured swim bladders in black sea bass. Further experimentation is needed to determine the effects of swim-bladder rupture on a species-specific basis.

It is likely that survivorship following release varies with depth due to hydrostatic factors alone. Regression of trawl-caught red snapper stomach eversion proportions on capture depth (values from the literature) explains 80% of the variance in the observed data (Fig. 1*A*; $r = 0.90$, df = 5, $P < 0.01$). Inclusion of our trawl-caught red snapper data rendered the relationship nonsignificant (Fig. 1*A*; $r = 0.70$, df = 6, $P < 0.05$). A similar plot of angling-caught red snapper data from the literature was not significant (Fig. 1*B*; $r = 0.58$; df = 5; $0.10 < P < 0.05$), possibly because of the differences in the sizes of red snappers hooked with respect to depth (see Figure 1 citations) and resultant differences in the rates of ascent, or ontogenetic differences in relative swim-bladder volume. Note that increased depth eventually outweighs any real effect of the size of the fish and tenacity of its struggle against the angling gear, or anatomical variation, rendering the overall relationship positive albeit nonlinear. The above data (Fig. 1*A*, *B*) also indicate that red snappers caught with any gear over bottoms <30 m deep do not suffer significant trauma. Similarly, depths ≤ 20 m introduced no difficulties to a food habits study of this species (Moseley 1966).

Clearly, regulations which diminish removal of fishes (e.g., gear/method restrictions, area/time closures) will be more effective over a larger depth range than release measures. Current management of the southeastern U.S. snapper-grouper fisheries guarantees subjection of protected size classes to stress and trauma. However, it is conceivable that swim-bladder deflation techniques could improve the effectiveness of current regulations.

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[6] D. M. Miller, Curator, University of Georgia Marine Education Center, POB 13687, Savannah, GA 31416, pers. commun. November 1984.

[7] R. O. Parker, National Marine Fisheries Service, Southeast Fisheries Center, Beaufort Laboratory, POB 500, Beaufort, NC 28516, pers. commun. October 1984.

The data we have presented show that the effects of capture on sponge-coral reef fishes vary between species and gears. These are important considerations for studies of feeding biology. Additional data on fish species survivorship following releases, stratified by gear and depth, will allow fine-tuning of present snapper-grouper management policies.

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ANNUAL PRODUCTION OF EVISCERATED BODY WEIGHT, FAT, AND GONADS BY PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*, NEAR AUKE BAY, SOUTHEASTERN ALASKA

JAY C. QUAST[1]

ABSTRACT

Pacific herring, *Clupea harengus pallasi*, grow according to the constant-proportion growth model, which requires that yearly growth in body length be a constant proportion of growth during the previous year. Herring have one or two growth stanzas (periods of constant-proportional growth) in the eastern Pacific Ocean and eastern Bering Sea, and grow faster in the eastern Bering Sea than in the northeastern Pacific Ocean.

With growth, total and eviscerated body weights of fresh Auke Bay herring bear an exponential relationship to body length (BL) that is slightly greater than cubic, and evisceration does not lower variability in length-weight relationships. With growth, an increasing part of the annual product (growth plus gonads) is partitioned into gonads so that in the largest fish most of the annual product is gonads. The annual product is constantly proportional to BL through ages 2-6 and also through ages 9-12, but the proportion is considerably smaller in the 9- to 12-yr-old fish. The two differing proportions may indicate that young and old Auke Bay herring occupy slightly different feeding niches and that the trophic environment in the Auke Bay vicinity may not support the older fish as well as the younger.

Pacific herring spawn in April or May in the Auke Bay vicinity, as zooplankton density rapidly increases to its peak in June. The time of spawning seems optimal for rapid building of fat reserves and feeding of newly hatched larvae.

Pacific herring, *Clupea harengus pallasi*, range off western North America, from the Chukchi Sea to San Diego, CA, and have been commercially exploited over the entire range (Rounsefell 1930; McLean and Delaney 1978; Spratt 1981). Pacific herring usually occupy extensive reaches of coast, from tens to hundreds of miles, and populations are particularly dense around the Alexander Archipelago of southeastern Alaska and the archipelago off British Columbia (from charts or fisheries maps in Rounsefell 1930, McLean and Delaney 1978, and Spratt 1981). Yet, even where dense, populations can be locally distinctive in vertebral number and spawning time (Rounsefell and Dahlgren 1935; Hourston 1980).

Pacific herring have been commercially harvested in Alaska since the late 1800's (Rounsefell 1930), principally for reduction to meal and oil. Herring were also pickled, starting in 1900, but the industry never became large and declined in the 1920's. A fishery for Pacific halibut, *Hippoglossus stenolepis*, bait had a similar rise and decline. The reduction fishery ended in the 1960's, and the principal fishery for Pacific herring in Alaska now is sac roe, which is exported to Japan.

The biology of Pacific herring in Alaska has not been thoroughly described. The study by Rounsefell (1930) is the most comprehensive work, and Rounsefell and Dahlgren (1935) separated stocks in southeastern Alaska on the basis of vertebral counts. Skud (1963) analyzed tag returns, and Carlson (1980) described the ecology of Auke Bay herring. Reid (1971) summarized some biological characteristics of herring taken for the reduction fishery from 1929 to 1966.

Because Pacific herring are economically and ecologically important in southeastern Alaska and there is little information on the growth, productivity, and life history of this species in this region, I undertook a 1-yr study of a population in the Auke Bay vicinity (Auke Bay is about 16 km northwest of Juneau). Goals of the study were to compare growth of Pacific herring in the Auke Bay vicinity with growth of Pacific herring from other locales in the eastern Pacific Ocean and relate annual production of fat, gonads, and eviscerated weight in the Auke Bay herring to the annual cycle of food supply.

Pacific herring of the Auke Bay vicinity are one of the innermost and northernmost populations in

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[1] Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821; present address: 1565 Jamestown Street S.E., Salem, OR 97302.

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the Alexander Archipelago (Auke Bay is about 80 nmi [148 km] by water from the open coast). Although this population may contain more than one spawning stock, it will be identified with Auke Bay in the present study (local populations spawn within weeks of each other and within a few nautical miles).

METHODS

Auke Bay herring were sampled several times monthly from April 1973 to March 1974; however, no fish were taken in February 1974. The fish were captured principally by jigging with bright hooks or hooks wrapped with colored yarn. Samples were also taken during spring 1973 from nearby locales in southeastern Alaska, including Hood Bay (off Chatham Strait, southwest of Juneau), Carroll Inlet (near Ketchikan), and Katlian Bay (near Sitka), and also from the eastern Bering Sea west of Nunivak Island.

Auke Bay herring were usually examined fresh but sometimes were frozen and examined within 1 wk. Lengths were originally measured as standard lengths (SL, tip of upper jaw to end of hypural bones) but were later converted to body length (BL, tip of lower jaw to end of hypural bones) by multiplying SL by 1.0132, the average ratio in 126 specimens from Auke Bay.

Body lengths were back-calculated from scales taken from above the pectoral fins and posterior to the opercular flap. The calculations followed the proportional method of Whitney and Carlander (1956), which should reduce the variation in BL-scale size relationships because the method adjusts for possible differences in scale length in the same-sized fish. This method requires that the regression between BL and scale length be linear, which was satisfied (Fig. 1). The intercept of the regression (55 mm) was somewhat higher than the median BL (36.5 mm) for first squamation of 16 preserved specimens; however, the differences between estimates for BL at first squamation are probably important only for fish younger than 1 yr. The regression fit the data well for herring ≥ 1 yr old (Fig. 1). I also attempted to reduce variability in the back-calculations for the Auke Bay fish by averaging focus-to-annulus distances from left and right sides of the scales (annuli were as well defined at the sides as in the centerline of the scale), but only a centerline measurement was used in samples from other geographic regions.

After the growth data were analyzed by Walford graphs (Walford 1946), linear regressions (Walford regressions) were fit by least squares to adult sections of constant parameters (stanzas) that were indicated on the graphs. Both the Walford regression and von Bertalanffy formulation are variants of the constant-proportion growth model, which requires that growth in one year be a constant proportion of growth the preceding year (Ricker 1975). (The slope of a Walford regression equals the von Bertalanffy e^{-K}, and the intercept equals $L_\infty(1 - e^{-K})$.)

Annual changes in development of fat and gonads were evaluated by indices that were derived from total body weights, eviscerated body weights, and gonad weights. I estimated unbound water in the eviscerated body tissues and gonads as the percentage weight lost by drying 1 cm wide transverse body sections and entire gonads in a drying oven for more than 4 d at 27°C, a period that yielded weight stability. Visual estimates of visceral fat used a four-point scale (from none to heavy), and visual estimates of maturity used a seven-point scale, as follows (Roman numerals in brackets refer to a similar scale developed by Hay and Outram (1981) for Pacific herring): 1) Newly regenerating [VIII], 2) regenerating [III], 3) nearly mature [IV], 4) ripe [V], 5) ripe and running [VI], 6) partially spawned [VII], and 7) spawned out [VII]. Fresh body, eviscerated, and gonad weights were regressed on body lengths by least squares after logarithmic transformation of variates. Statistical tests were significant when $P < 0.05$.

Scales of Pacific herring from southeastern Alaska and the eastern Bering Sea probably have two annuli in the first growth year. When the annulus nearest to the scale focus of Auke Bay herring was used for back-calculations, the BL's were much smaller (average of 65 mm) for the first winter than the BL's of juvenile herring (at least 80 mm) captured at the end of their first year in Auke Bay by Jones (1978). Pacific herring in British Columbia attain a length of at least 80 mm by their first September (Hourston 1958). Furthermore, when the first annulus was used as the first year mark, Walford graphs of the growth data were erratic and differed markedly from graphs of the same type of data in the literature. When the second annulus was used as the first year mark, the graphs were simple and corresponded to graphs of similar data from the literature.

There was no indication of Lee's phenomenon (slower growth in longer lived individuals) in the back-calculated BL's, but there was evidence of a changing relation between growth back-calculated for ages 1 and 2 and the span of years that was used

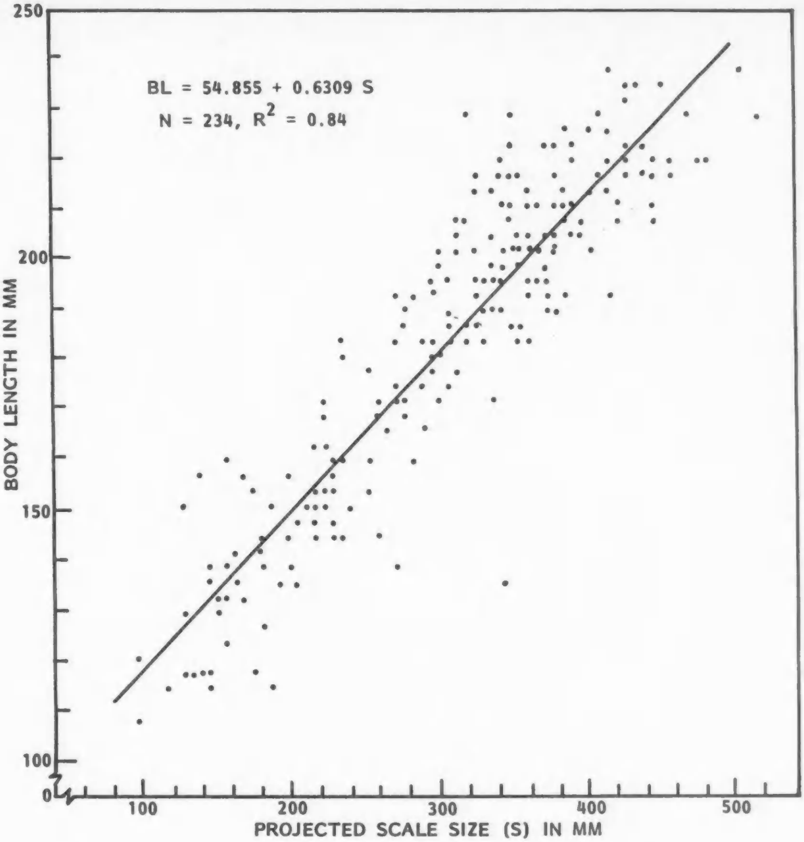

FIGURE 1.—Relationship between body length (BL) and projected scale size (S) of Pacific herring from Auke Bay, AK.

in the back-calculations. When the estimates of growth to ages 1 and 2 were compared for all specimens, those from herring aged 2-4 at time of capture (back-calculated over a span of 0-2 yr) had slower-than-average growth, and those herring aged 4-7 (back-calculated over a span of 3-5 yr) had faster-than-average growth (Fig. 2). Estimates for the oldest herring (back-calculated over a span of ≥6 yr), however, gave mixed results. The trends in fish of 5 yr and younger may have been caused by environmental influences because the trends occur in sets of years (fish aged 2-4, when captured, spent their first or second growth years in 1970-72, and those aged 4-7 spent their first or second growth years principally in 1966-69).

GROWTH

The average size-at-age data in my samples of Pacific herring from the eastern Pacific and eastern Bering Sea and data from the literature for those regions usually formed two stanzas on Walford graphs and inflected at ages 2 or 3 (see Figure 3 for examples). The data for Norwegian and Murman stocks of Atlantic herring, *Clupea harengus harengus*, (Svetovidov 1952) also formed two stanzas and intersected at age 2. Although the stanzas for all of my back-calculated data from the eastern Pacific Ocean intersected at age 2, stanzas for two populations from California (data from Spratt 1981) intersected at age 3, and a plot of Naumenko's

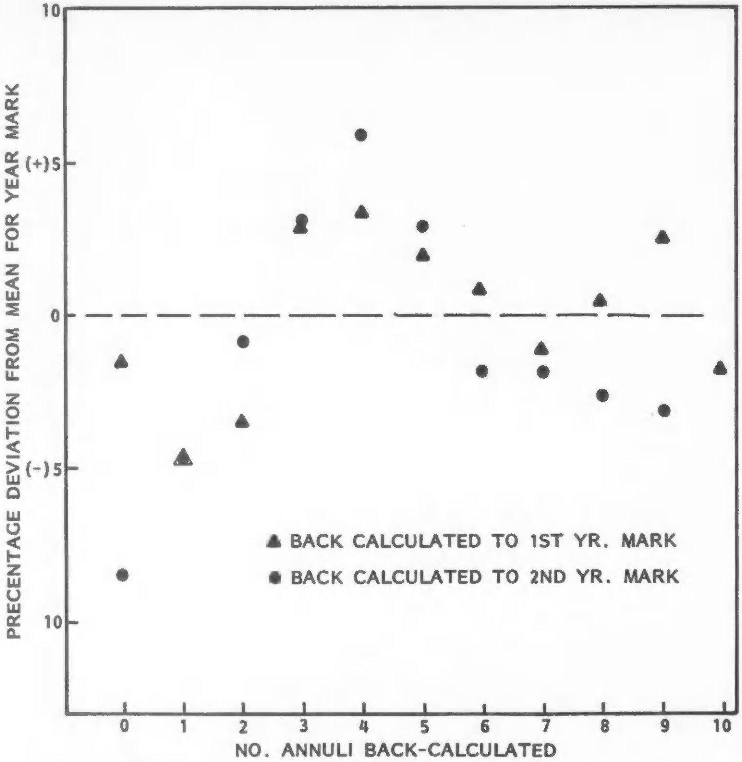

FIGURE 2.—Relationship between extent of back-calculation from scales and the body length estimated at 1 and 2 yr in Pacific herring from Auke Bay, AK. Points indicate the deviation of size estimates for age-1 and age-2 Pacific herring from the average for all annuli (the second annulus was taken as the first year's mark).

(1979) data from the eastern Bering Sea had only one stanza. Regardless of the data source, linear regressions (Walford regressions) closely fit the data in the growth stanzas (Tables 1, 2).

The method of aging Pacific herring can influence estimates of growth. In the data that I examined for this study, adult stanzas based on back-calculated lengths usually had lower slopes than adult stanzas based on terminal-lengths-at age (Table 1). Furthermore, the plots of back-calculated data inflected either at 2 yr or not at all, in contrast to plots of lengths-at-terminal-age, which inflected at 3 yr in three of six examples (Table 1). Important factors, however, remain uncontrolled in this comparison. For instance, the lengths-at-terminal-age from the literature were based on summer sampling; hence, they include additional growth after annulus formation. The lengths-at-terminal-age were from populations near or on the open coast, which may grow faster than populations from protected and possibly less productive waters within the Alexander Archipelago. Furthermore, it is not clear that the Alaskan data for lengths-at-terminal-age used the second scale annulus as the first year's mark.

Walford graphs for Pacific herring from Tomales Bay, CA (data from Spratt 1981), and the eastern Bering Sea (this study) indicated that juvenile growth success and age at inflection (intersection of juvenile and adult stanzas) are more important determinants of adult size at age than either length at year 1 or the slope of the adult stanza, the adult growth proportion (Table 1; Fig. 3). The data indicate that herring from the Bering Sea quickly outgrow those from Tomales Bay although the BL's of the two groups were almost identical at ages 1

TABLE 1.—Growth characteristics and growth parameters of Pacific herring from the northeastern Pacific Ocean and eastern Bering Sea, based on data from the present study and from the literature. Growth is portrayed by the Walford version of the constant-proportion growth model (see text). Because Reid's (1971) data were gathered from a summer fishery, body lengths are longer than they were at the time of annulus formation and may not be comparable to back-calculated data or to lengths-at-terminal-age collected on or near the time of annulus formation. The inflections column refers to the junction of juvenile stanzas with stanzas for adults. Juvenile stanzas on the Walford graphs were fit by eye to sizes at ages 1 and 2, or ages 1-3; adult stanzas were fit by least squares.

Capture location	Size at age 1 (mm)	Inflection at year	Adult stanza			Aging method	Source
			Intercept	Slope	R^2		
Back-calculated lengths:							
Auke Bay vicinity	93.3	2	64.89	0.709	0.998	scales	this study
Hood Bay, Chatham Strait	90.8	2	66.31	0.664	0.995	scales	this study
Katlian Bay	101.5	2	81.50	0.659	0.991	scales	this study
Carroll Inlet	102.7	2	83.61	0.632	0.999	scales	this study
Eastern Bering Sea	112.8	2	79.26	0.727	0.993	scales	this study
Eastern Bering Sea	90.3	?[1]	88.79	0.722	0.999	scales	Naumenko 1979
Lengths-at-terminal-age:							
Auke Bay vicinity	—	2	64.94	0.716	0.983	scales	Blankenbeckler 1979[2]
Prince William Sound, AK	131.4	3	40.60	0.859	0.985	scales	Reid 1971
Kodiak vicinity, AK	132.1	2+	55.99	0.792	0.990	scales	Reid 1971
Southeastern Alaska	145.1	2+	52.14	0.788	0.967	scales	Reid 1971
San Francisco, CA	113	3	44.87	0.816	0.989	otoliths	Spratt 1981
Tomales Bay, CA	113	3	36.95	0.871	0.996	otoliths	Spratt 1981

[1] No inflection apparent.

[2] Blankenbeckler, D. 1978. Age, growth, maturation, and parasite occurrence of Pacific herring (*Clupea pallasi*) from southeastern Alaska, 1974 through 1976. Alaska Dep. Fish Game, Tech. Data Rep. 39, 88 p.

and 2, and the adult stanza was steeper for herring from Tomales Bay. The Bering Sea herring, however, inflected to a steeper slope at age 2 rather than age 3. Environment may not determine the time of inflection in Pacific herring because juveniles both from the Bering Sea and Tomales Bay had similar BL's during the first 2 yr (Fig. 3) although the environments of the locales probably differ greatly.

Weight-Length Relationships

Total weight (W, grams) relates to BL (millimeters) in fresh Pacific herring from the Auke Bay vicinity as $W = (4.4467 \times 10^{-6})\mathrm{BL}^{3.2232}$ ($N = 491$; $R^2 = 0.97$). The lower confidence limit for the exponent exceeds 3.0, and the exponent exceeds 3.0 in reports for herring in most locales; e.g., Pacific herring from Tomales Bay, 2.93 (Spratt 1981); San Francisco Bay, 3.23 (Spratt 1981); the east coast of Vancouver Island, 3.26 (Hart et al. 1940), and Barkley Sound, British Columbia, 3.46 (Hart et al. 1940); and in Atlantic herring, 3.15 and 3.5 (Hart et al. 1940). Many differences between exponents, as cited, may not be biologically significant because weight-length relationships vary seasonally and between sexes, even in eviscerated fish. The exponent for the relationship between BL and total weight probably exceeds 3.0 in healthy herring populations because, as noted in later paragraphs, both eviscerated and gonad fresh weights also have exponents >3.0 when related to BL.

Eviscerated weight of Auke Bay herring also had an exponential relationship to BL that significantly exceeded 3.0 [$(W = 5.0894 \times 10^{-6})\mathrm{BL}^{3.16640}$; Fig. 4]. In theory, evisceration avoids large potential weight variations caused by seasonal changes in gonads and fat deposits about the viscera, and variable food content; yet, eviscerated weight ($Sy \cdot x = 0.1030$) was at least as variable a function of BL as total weight ($Sy \cdot x = 0.0953$) in the same specimens, and both total weight and eviscerated weight had the same coefficient of determination (0.97). The lack of decreased variability in the weight of eviscerated herring, as a function of BL, compared with whole fish is evidence that building of visceral fat and gonads does not simply add weight, but rather that some compensatory mechanism may act between these apparent weight sources and the eviscerated body.

In contrast to the results of Hart et al. (1940), Hickling (1940) found markedly low exponents, 2.13 and 2.37, for the relationship between eviscerated weight and BL for Atlantic herring from the North Sea, values that are strikingly lower than those expected for fishes in general. For example, Quast (1968) gave exponents of 2.7-4.5 for 32 species of marine fishes in southeastern California, including 3.9 for the northern anchovy, *Engraulis mordax*. Hickling's exponents may be too low because the

TABLE 2.—Body lengths (BL's) of Pacific herring from the Alexander Archipelago and the eastern
data) or mean back-calculated BL's; fitted lengths are predicted by the constant-proportion grow
<5 (found data) or extrapolations with the growth models. Average differences between the fitte
values in parentheses. For Pacific herring in the Auke Bay vicinity, average differences betwee
on back-calculations (col. 5) was 1.96%.

			Bac			
	Terminal lengths (mm) Auke Bay vicinity		Auke Bay vicinity		Hood Bay, Chatham Strait	
Age	Found	Fitted	Found	Fitted	Found	Fitted
1	—	—	93.3	—	90.8	—
2	133.0	—	130.8	131.0	125.9	126.6
3	163.6	160.2	159.2	157.8	151.9	150.4
4	176.0	179.6	178.0	176.8	165.6	166.2
5	190.6	193.6	189.5	190.2	175.1	176.6
6	203.7	203.5	198.0	199.8	183.7	183.6
7	211.5	210.7	203.6	206.5	(181.1)	(188.2)
8	215.6	215.8	209.2	211.3	(186.1)	(191.3)
9	219.9	219.4	214.5	214.7	—	(193.3)
10	220.7	222.0	217.8	217.1	—	(194.7)
11	225.4	223.9	221.2	218.8	—	(195.6)
12	(213.2)	(225.3)	220.9	220.0	—	(196.2)
13	(231.7)	(226.2)	(229.3)	(220.9)	—	(196.6)
Average difference (%)	0.86		0.66		0.56	

[1]Blankenbeckler, D. 1978. Age, growth, maturation and parasite occurrence of Pacific herring (*Clupea pa*
Data Rep. 39, 88 p.

astern Bering Sea, AK. Found lengths are mean BL's at capture (Blankenbeckler's[1] on growth model (see text) from found lengths. Parentheses indicate sample sizes he fitted and found data (bottom line) were based on absolute values and exclude between fitted lengths based on length at capture (col. 3) and fitted lengths based

Back-calculated lengths (mm)					
Katlian Bay		Carroll Inlet		Eastern Bering Sea	
Found	Fitted	Found	Fitted	Found	Fitted
101.5	—	102.7	—	112.8	—
153.3	152.3	148.5	148.5	163.3	161.3
182.6	181.9	176.7	177.5	198.4	196.5
196.7	201.4	196.9	195.8	221.4	222.1
213.4	214.2	208.9	207.3	236.5	240.7
223.6	222.7	214.4	214.6	247.8	254.3
228.7	228.2	219.2	219.3	261.2	264.1
(223.4)	(231.9)	(221.5)	(222.2)	274.2	271.3
—	(234.3)	(220.9)	(224.0)	(284.4)	(276.5)
—	(235.9)	(223.8)	(225.2)	(288.4)	(280.3)
—	(237.0)	(229.0)	(225.9)	(293.0)	(283.0)
—	(237.7)	(248.2)	(226.4)	—	(285.0)
—	(238.1)	—	(226.7)	—	(286.5)
0.73		0.32		1.28	

upea pallasi) from southeastern Alaska, 1974 through 1976. Alaska Dep. Fish and Game Tech.

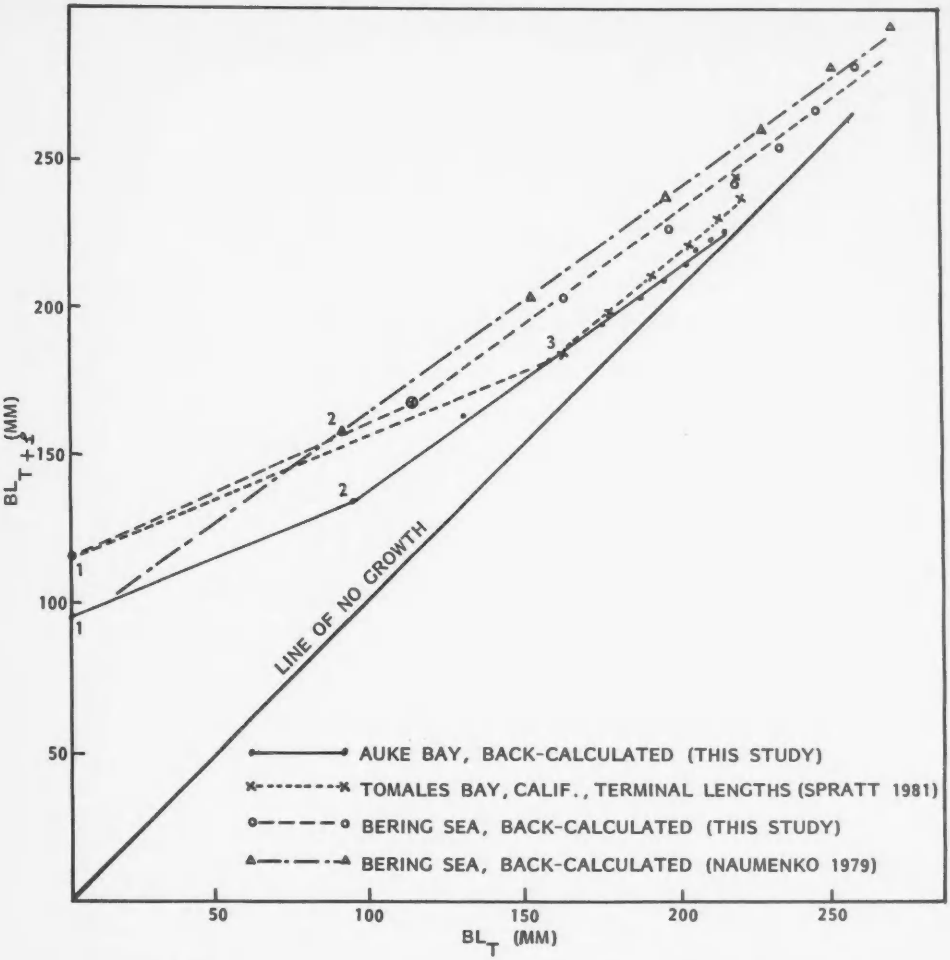

FIGURE 3.—Examples of Walford trends in body length of Pacific herring from widely separated locales in the eastern Pacific Ocean and Bering Sea. Heavy solid line through origin is the line of zero growth, and numbered points indicate ages in years. Adult stanzas were fit by least squares, and the juvenile stanzas were fit by eye. Data from Naumenko (1979) represent 25 yr of collections.

effective range of BL's was limited (near 50 mm) in his data sets and his data were grouped in 10 mm size classes. (In contrast, BL's extended over about 130 mm in the Auke Bay herring, and lengths were taken to 1 mm.)

In Pacific herring, the relationship between eviscerated weight and BL varies with season and sex (Fig. 5), and the relationship for Atlantic herring should vary similarly. Although Hickling (1940) concluded that regressions of eviscerated weight on BL differed by sex in Atlantic herring ($W = 0.0661$ $BL^{2.312}$ in males, and $W = 1.1471$ $BL^{1.456}$ in females), his samples probably were too restricted seasonally to estimate reliably the relationship between eviscerated weight and BL for all seasons. Because of seasonal variation in fat content of the musculature (discussed in the next section), data for a single season cannot represent an average over all seasons in Pacific or Atlantic herring of either sex.

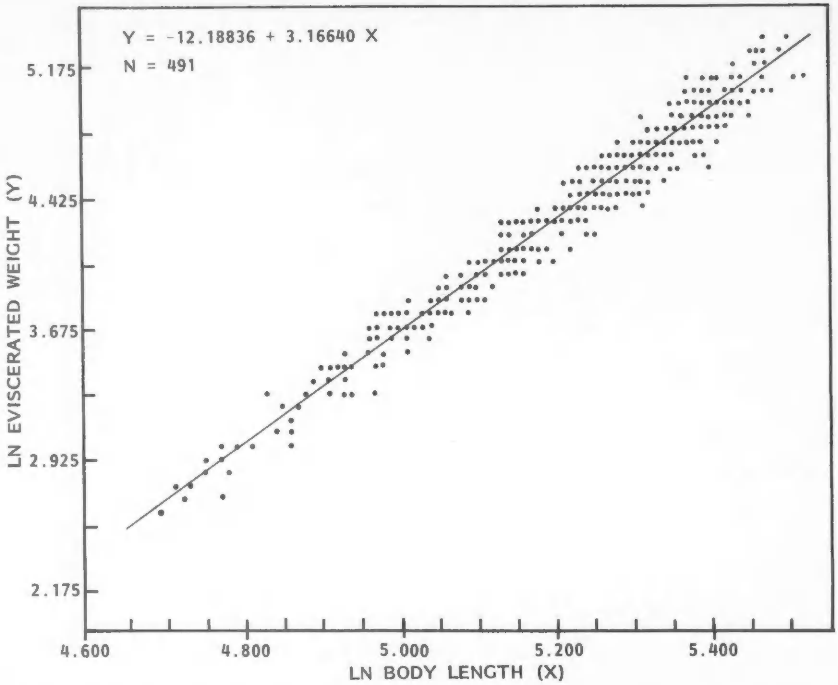

FIGURE 4.—Relationship between body length and eviscerated body weight in fresh Pacific herring in the vicinity of Auke Bay, AK, sexes combined. Variates transformed to their natural logarithms (LN). Points represent 1-9 specimens.

Seasonal Cycles in Fat and Gonads

Adult Pacific herring feed chiefly on zooplankton and small fishes (Hart 1973). In the Auke Bay vicinity, zooplankton peak in abundance in June or July and are virtually absent from November to March (Fig. 6; fig. 3 in Carlson 1980). In an unpublished study of Auke Bay herring, stomachs were mostly empty during late fall and winter (R. E. Haight, cited in Carlson 1980).

Pacific herring spawn in Auke Bay in late April or May but may spawn as late as 4 June (Wing[2]). Eggs hatch 14-20 d after spawning, based on incubation temperatures for herring in British Columbia (Outram 1965[3]) and temperatures for mid-April and May in Auke Bay, which are similar to those for British Columbia (Wing[4]). The time of spawning seems optimal to allow spawned fish and their newly hatched larvae to feed during the heaviest zooplankton concentrations of the year (Fig. 6).

Because the peak in zooplankton abundance is relatively brief, the period immediately after spawning is critical for fattening of adults and for growth and survival of newly hatched larvae. Feeding and fattening of all life stages of Auke Bay herring may also be aided by the submarine illumination afforded by the longest days and highest levels of light, early in the summer.

Fat accumulated about the viscera during the period of maximum zooplankton abundance and reached highest indices shortly afterward, about mid-July (Fig. 6). It then declined rapidly but slightly differently in each sex. There is evidence, also, based

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[2] B. L. Wing, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. November 1981.

[3] Outram, D. N. 1965. Canada's Pacific herring. Dep. Fish. Can., Ottawa, Fish. Res. Board Can., Biol. Stn., Nanaimo, B.C., 23 p.

[4] B. L. Wing, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. July 1983.

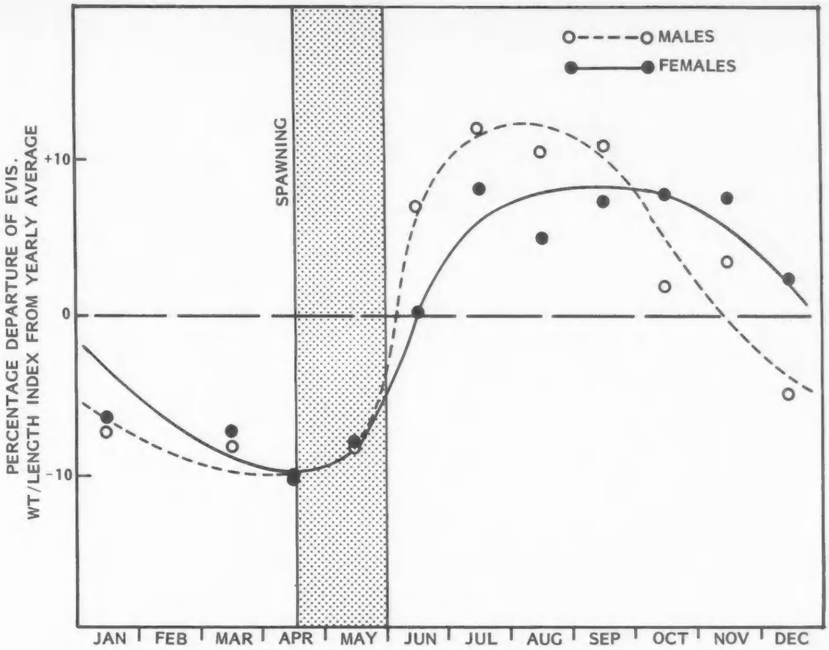


FIGURE 5.—Seasonal variation in eviscerated weight as shown by monthly samples of fresh Pacific herring near Auke Bay, AK, given as percentage departure from the weight predicted by the general eviscerated weight/BL regression for these fish (see Figure 4). The percentage departure is given relative to its yearly average to highlight seasonal changes. Data fit by eye.

on the water content of the musculature, that intramuscular fat varied seasonally and paralleled the development of visceral fat—water content of eviscerated body sections for the sexes behaved in an opposite fashion to visceral fat, being highest in April-May and at low levels between June and October (Table 3). In contrast to the water content of the musculature, eviscerated weight increased relative to BL after May (Fig. 5). If the increase in eviscerated weight were caused by increased somatic hydration, variation in hydration would have paralleled variation in eviscerated weight, but instead, the values for hydration decreased after May. Some other factor must be responsible for the increased eviscerated weights after May, and a likely candidate is fat, because eviscerated weight increased over the same period that visceral fat was building. Hart et al. (1940) also described an apparent reciprocal relationship between water and oil content in Pacific herring from British Columbia, and Love (1970) discussed the same relationship in Atlantic herring and other fish species with fatty tissues.

TABLE 3.—Average hydration of musculature as a percentage of wet weight, by month in Pacific herring from Auke Bay, AK.

	Males		Females	
Month	*N*	Percent	*N*	Percent
January	15	69.2	6	68.4
March	17	71.1	19	71.0
April	26	75.3	25	76.0
May	29	77.0	29	76.0
June	8	61.7	12	66.5
July	8	60.8	12	61.5
August	10	60.7	10	61.1
September	23	61.7	30	62.7
October	12	61.9	18	61.5
November	1	62.6	6	60.6
December	3	65.0	25	63.1

The timing of gonad development, as indicated by seasonal development of gonads, differed in the sexes in Pacific herring from Auke Bay. Males were

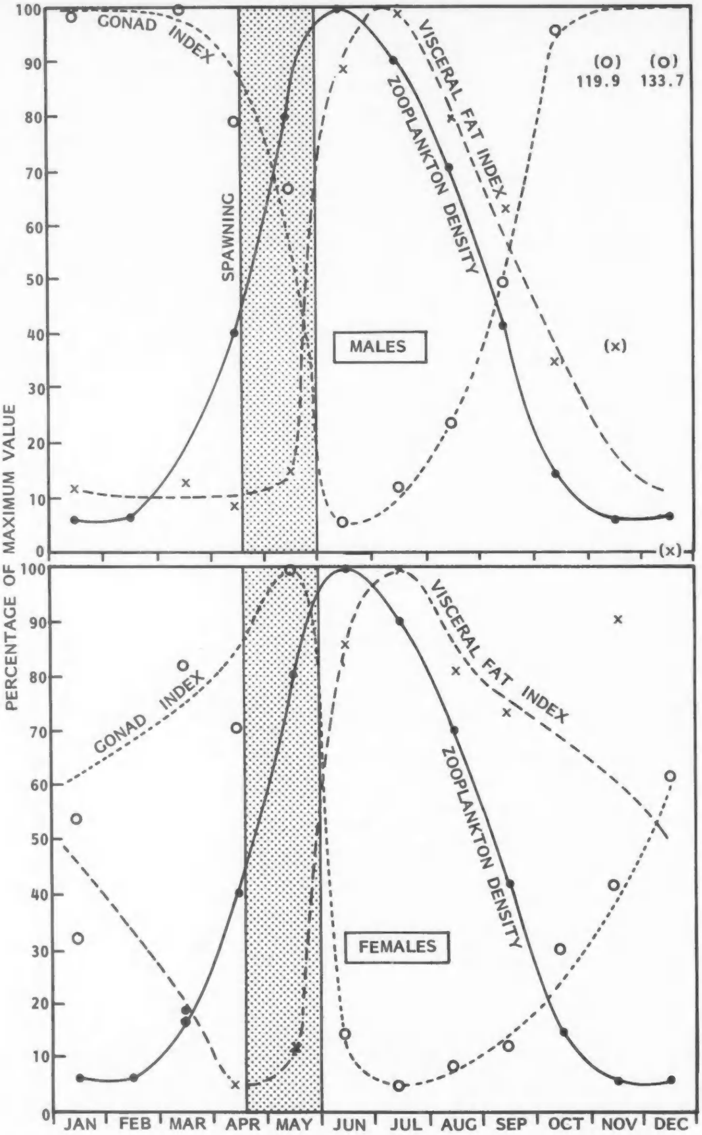


FIGURE 6.—Three annual cycles that relate to the condition of Pacific herring in the vicinity of Auke Bay, AK: A visual index of visceral fat (see text); gonad indices based on (wet) gonad weights as a percentage of the eviscerated (wet) body weights that would be expected at various BL's (see Figure 4); and an annual cycle of zooplankton density, from displacement volumes for 1962-64 given in Wing and Reid (1972). Points based on less than five specimens are enclosed in parentheses. Curves fit by eye.

nearly ready to spawn in November but females delayed readiness until perhaps 4 mo later (Fig. 6), a delay that was confirmed by visual judgments of maturity, see table below (sample size in parentheses):

Percentage of herring judged ripe

	Sept.	*Oct.*	*Nov.-Jan.*	*Mar.*
Males	4(23)	92(12)	95(19)	94(18)
Females	0(31)	11(18)	79(38)	90(20)

These data differ in some important respects from those of Hay and Outram (1981) for Pacific herring in British Columbia. Their gonadosomatic index has sharper peaks in maturity of gonads and different timing of the peaks than the Pacific herring from Auke Bay. For example, in their data, testes were only developing (a low gonadosomatic index) in October (the fish spawned in late February and early March), but testes were near maximum fullness (high index values) in October in herring from Auke Bay (Fig. 6). However, Hay and Outram used total weight in their index. If total weight is used for the index, the divisor will include a considerable weight of fat about the viscera in the fall and negligible weight in the spring, with the result that even if gonad weights remain the same from November to February, the decline in the amount of fat would cause the index to increase. In my study of the Pacific herring in Auke Bay, I divided gonad weight by eviscerated body weight, which should avoid an appreciable error in the gonadosomatic index that would be caused by variation in visceral fat.

Within each sex, seasonal profiles for gonad indices are nearly opposite the profiles for indices of visceral fat (Fig. 6). The annual cycles in fat and gonad indices (Fig. 6) in Pacific herring from Auke Bay resemble those noted by Blaxter and Holliday (1963) for spring spawning in Atlantic herring: "In winter-spring herring the good feeding conditions in late spring and early summer (after spawning) build up the fat reserves. With development of the gonads in late autumn feeding stops and spawning in December-March means that the fish overwinter and spawn with fat reserves considerably lower than the autumn spawners." Visceral fat in male Auke Bay herring is lowest in winter (perhaps as early as November), but in females does not reach lowest values until April. Correspondingly, the testes build rapidly in late summer and fall and appear to be heaviest by October or shortly after, but the ovaries are not at their heaviest until shortly before spawning, in April or May. Hydration is not responsible for sexual differences in development of gonad weight from January to March because, as the following table indicates, hydration remains virtually constant from November to March in both sexes (Table 4).

TABLE 4.—Average hydration of gonads, as a percentage of wet weight, by month in Pacific herring from Auke Bay, AK.

Month	Males		Females	
	N	Percent	*N*	Percent
January	14	76.2	5	73.6
March	16	76.1	17	71.3
April	39	82.6	33	84.5
May	24	83.7	24	77.2
June	6	75.5	9	77.7
July	18	73.6	19	76.2
August	25	77.9	21	80.7
September	19	77.6	25	78.6
October	12	76.9	18	74.5
November	1	76.1	6	72.7
December	3	74.2	25	71.2

This seasonal, mirror imagery between development of fat and gonads, with the images differing for sexes, is evidence for a strong physiological coupling between fat depots and gonads. Fat depots enable Pacific herring to accommodate two critical cycles in their life history that are badly out of phase: The zooplankton cycle, with its brief, summer peak that builds fat depots rapidly and is followed by low levels of food abundance from October to March; and the gonad cycle that slowly removes fat from the depots with the slow building of testes from July through October and the slower building of ovaries from July through March.

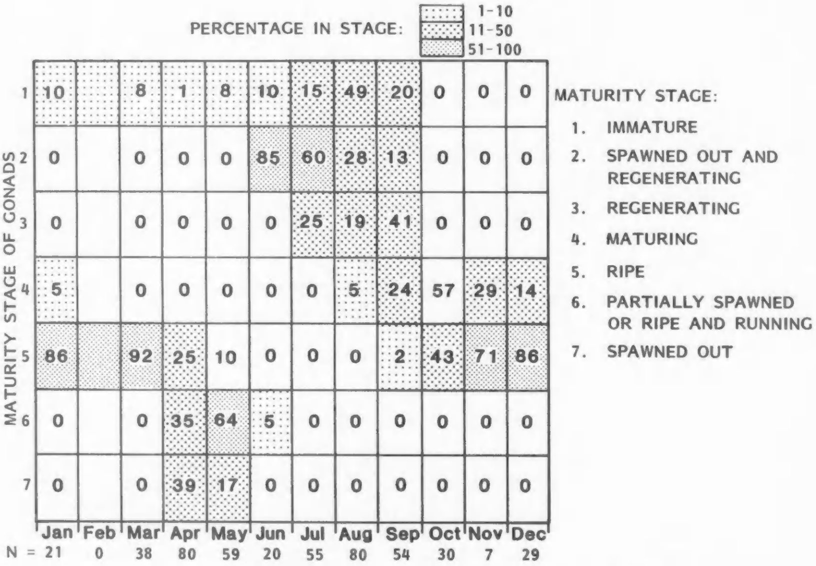
Are the seasonal cycles of gonad maturity in Pacific herring from Auke Bay determined by genetics or are the gonads responding principally to cyclical changes in the immediate environment? Iles (1984) felt that Atlantic herring are remarkably independent of their environment. Genetic control of gonad maturity seems likely except for spawning, which appears to respond to local temperatures (Outram 1965, see footnote 3). Gonads must build well in advance of spawning, and spawning dates vary from November in the southern limits of the eastern Pacific range (Spratt 1981) to June in Auke Bay. Female Auke Bay herring mature sexually and use fat deposits later in the fall than do males and thus anticipate a later spawning date. Male herring in the eastern Pacific Ocean, in contrast, appear to build testes early enough to spawn at any date between November and June. Only the ovarian cycle seems to correspond closely to the local environmental conditions that seem optimal for larval growth and survival. Possibly, the genes that are responsible for local adaptation of spawning stocks are sex linked for females and are selected through larval survival.

Annual Production of Eviscerated Weight and Reproductive Tissues

Although Pacific herring usually have only one major spawning per site in the Auke Bay vicinity, there may be a succession of lesser spawnings each spring. Unspawned fish are rarely seen as late as July (author's observations and comments by salmon fishermen who jig herring for bait). Although Wing (see footnote 2) recorded spawnings in Auke Bay between 24 and 29 April 1973, herring must spawn for at least 2 mo in Auke Bay because some fish sampled in 1973 were partially spawned or ripe and running in May and June (Fig. 7). Presumably, local conditions influence the number of eggs deposited on any date.

The relationship between fecundity, as indicated by mature ovarian weight, and BL was greater than cubic, in agreement with data on other clupeiod species (Blaxter and Hunter 1982). Samples of Auke Bay herring had an exponent of 3.94 (Fig. 8), within the range (3.07-4.50) for Atlantic herring as given by Paulson and Smith (1977), from the literature. These authors gave an exponent of 3.32 for Pacific herring they sampled in Prince William Sound. Perhaps, the exponent for fecundity would have been higher for the herring Paulson and Smith sampled in Prince William Sound had their collections included smaller fish (their smallest were near 180 mm long, but fish as small as 130 mm were available in samples from Auke Bay). The exponent for testicular weight was considerably higher than that for ovarian weight in Auke Bay herring (Fig. 8); however, the difference may not be real because the confidence limits for the two exponents overlapped considerably.

The scatter in the plots of gonad and testes weights on BL for Auke Bay herring (Fig. 8) and for Pacific herring from Prince William Sound (fig. 1 in Paulson and Smith 1977) indicate that some of the herring may have been partially spawned when they were collected (fully spawned fish were not used in my data). If samples for fecundity are taken in the spawning season, there is the risk that some



PERCENTAGE IN STAGE:
░ 1-10
▒ 11-50
▓ 51-100

MATURITY STAGE OF GONADS	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	10		8	1	8	10	15	49	20	0	0	0
2	0		0	0	0	85	60	28	13	0	0	0
3	0		0	0	0	0	25	19	41	0	0	0
4	5		0	0	0	0	0	5	24	57	29	14
5	86		92	25	10	0	0	0	2	43	71	86
6	0		0	35	64	5	0	0	0	0	0	0
7	0		0	39	17	0	0	0	0	0	0	0
N =	21	0	38	80	59	20	55	80	54	30	7	29

MATURITY STAGE:

1. IMMATURE
2. SPAWNED OUT AND REGENERATING
3. REGENERATING
4. MATURING
5. RIPE
6. PARTIALLY SPAWNED OR RIPE AND RUNNING
7. SPAWNED OUT

FIGURE 7.—Maturity of Pacific herring near Auke Bay, AK, by month (sexes combined). Numbers in boxes are percentages of herring that were visually classified into maturity stages on examination. Total fish by month are given in the bottom line. Data for February were extrapolated from January and March.

fish will have spawned partially and that fecundity estimates will be too low.

When the relationships between BL, weight, and fecundity in Pacific herring from Auke Bay were used in a model of annual changes in gonad weight and eviscerated weight, production of eviscerated weight decreased rapidly with age or size (Table 5, col. 3). Gonad production (Table 5, col. 4), in contrast, increased yearly but appeared to approach an asymptote at about 31-34 g in the oldest fish. With age, more of the annual product (annual increment in eviscerated weight plus gonad weight) was par-

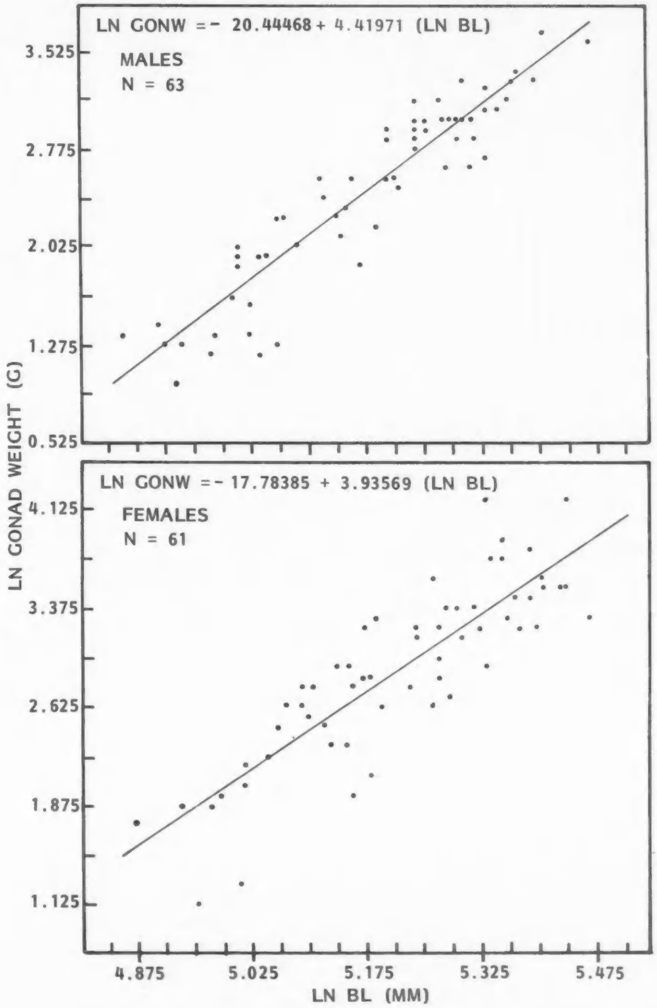


FIGURE 8.—Relationships between (wet) gonad weight (GONW) and BL in fresh Pacific herring collected from March to May 1973 near Auke Bay, AK (variates transformed by natural logarithms (LN). Data (not shown) that formed a separate cluster of points near the abscissa for each sex probably represented spawned fish and were not used in the regressions. Points represent 1-2 specimens.

TABLE 5.—Annual production of (wet) eviscerated weight and gonads in Pacific herring from the vicinity of Auke Bay, Alaska, as estimated from growth, length, and eviscerated-weight relationships, and length and gonad-weight relationships (Table 1, Figs. 4, 8). Column numbers are referenced in the text.

Annulus	(1) Fitted BL (mm)	(2) Estimated eviscerated weight (g)	(3) Eviscerated weight increment (g)	(4) Maximum gonad weight March-May		(5) Annual product (gonads plus eviscerated body weight)		(6) Annual product (5) as a percentage of BL the preceding year		(7) Annual product (5) as a percentage of eviscerated weight the preceding year		(8) Gonads as a percentage of annual weight product (5)	
				Males (g)	Females (g)	Males (g)	Females (g)	Males	Females	Males	Females	Males	Females
2	131.0	25.8	—	—	—	—	—	—	—	—	—	—	—
3	157.8	46.4	20.6	6.9	8.3	27.5	28.9	21	22	107	112	25	29
4	176.8	66.5	20.1	11.3	13.2	31.4	33.3	20	21	68	72	34	40
5	190.2	83.9	17.4	15.6	17.7	33.0	35.1	19	20	50	53	47	50
6	199.8	98.0	19.1	19.5	21.4	38.6	40.5	20	21	46	48	50	53
7	206.5	108.8	10.8	22.5	24.4	33.3	35.2	17	18	34	36	68	69
8	211.3	117.0	8.2	24.9	26.7	33.1	34.9	16	17	30	32	75	76
9	214.7	123.1	6.1	26.7	28.4	32.8	34.5	15	16	28	29	81	82
10	217.1	127.5	4.4	28.1	29.7	32.5	34.1	15	16	26	28	86	87
11	218.8	130.7	3.2	29.1	30.6	32.3	33.8	15	16	25	27	90	90
12	220.0	133.0	2.3	29.8	31.3	32.1	33.6	15	15	25	26	93	93

titioned into gonads, which by age 12 composed nearly all of the annual production (Table 5, col. 8). As the herring grew, the annual product was more closely related to BL than to eviscerated body weight (Table 5, cols. 6, 7), evidence that individual herring in the Auke Bay vicinity may use food more in proportion to their BL than their weight. Furthermore, although the relationship between annual product and BL was nearly constant within age groups 3-6 and 8-12 (Table 5, col. 6), productivity was much lower in the 8-12 group. Young Auke Bay herring may be more successful for their size in finding food than are older individuals, because important foods needed by older herring may be scarce in the Auke Bay vicinity, which is about 80 nmi (148 km) by water from the open ocean.

There is indirect evidence from the characteristics of growth and production in Auke Bay herring and growth characteristics of other Pacific herring in the northeastern Pacific Ocean and Bering Sea that not only growth but the annual product relative to herring size and the partitioning of the annual product may vary with the population. If the relationship between eviscerated weight and BL in Auke Bay herring is used with growth data of Pacific herring from other locales in the eastern Pacific Ocean and Bering Sea (Table 1), striking differences are visible in the annual product of eviscerated weight (Fig. 9). For example, if 190 mm herring (3-yr-olds) in the Bering Sea produce gonads in the same proportion to eviscerated weight as 190 mm herring in Auke Bay (5-yr-olds; Table 5, col. 8), gonads and eviscerated weight would each form about one-half of the annual product of Bering Sea herring. However, this proportion would be much too high for herring in Bering Sea during their first year of gonad production, according to the model based on Auke Bay herring, if Bering Sea herring mature as 2- or 3-yr-olds. If production of eviscerated weight and gonads is scheduled according to age, rather than proportion of annual product, similar conflicts result; thus, Pacific herring from different regions probably differ in characteristics for production of eviscerated weight and gonads.

CONCLUSIONS

Pacific herring grow in the eastern Pacific Ocean according to the constant-proportion model; i.e., growth in one year is a constant proportion of the amount grown the previous year. Growth stanzas (regions of constant growth parameters) for juveniles and adults usually inflect near age 2, and the change in growth is probably related to sexual

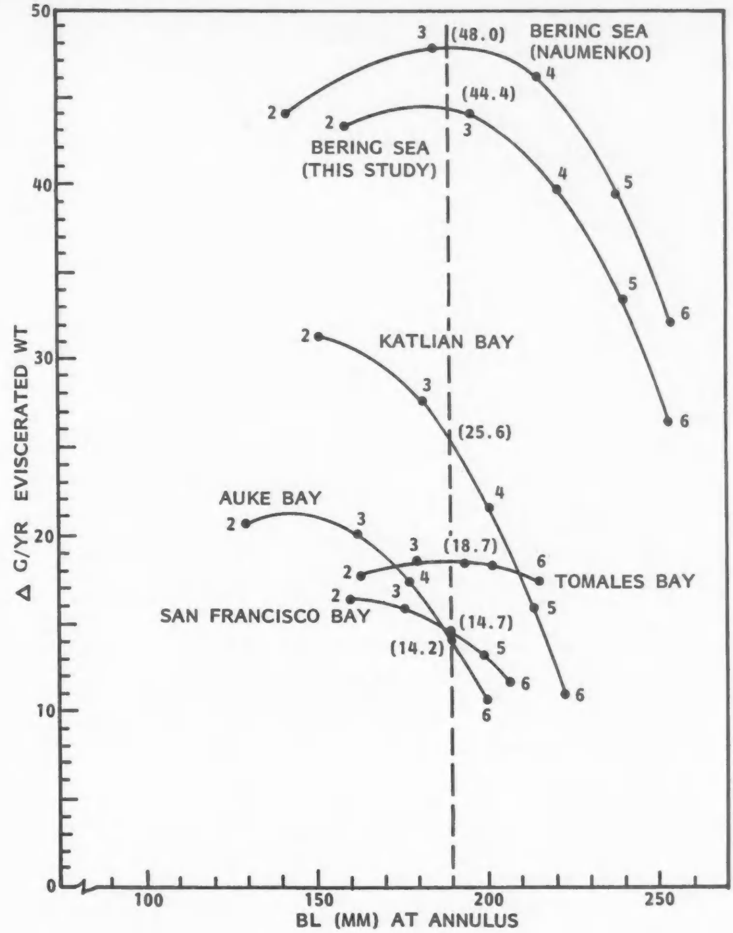


FIGURE 9.—Hypothetical growth in (fresh) eviscerated body weight by Pacific herring at locales in the eastern Pacific Ocean and eastern Bering Sea. Data were based on relationships between eviscerated body weight and BL in samples from the Auke Bay vicinity and data on growth reported in the literature (see Table 1). Numbered points are ages at the beginning of annual growth increments. The dashed vertical line is for comparative purposes and intersects the graphs at 190 mm BL. The second annulus was taken as the first year mark in specimens from Auke Bay, Katlian Bay, and Bering Sea (this study).

maturity. Size of adults is influenced more by growth rate of juveniles and the size at inflection of growth stanzas than by the constant of proportional growth after inflection.

In the Auke Bay vicinity, a sharp increase of zooplankton abundance in June is the determinent for the annual cycles of fattening and spawning in Pacific herring, and spawning in April or May seems optimally timed for growth of newly hatched fry. In summer, fat builds rapidly about the viscera and in the musculature of adults, as a reserve for gonad development and metabolism in fall and winter when food is scarce and herring do not feed. Iles (1984) found that in Atlantic herring fat is assimilated and deposited almost unchanged during the feeding cycle and is not utilized for metabolism until the metabolic pool of protein is exhausted. He also hypothesizes that annual somatic growth declines with gonad growth and ceases with depletion of the protein pool.

Male Pacific herring from Auke Bay build gonads and use their fat reserves more rapidly than do females. Testes may be near spawning condition in November, but ovaries are not full sized until April. Males may be ready or nearly ready to spawn in November over the entire eastern Pacific Ocean, but females delay spawning until local conditions of temperature and food abundance are optimal for larval growth.

The exponents for total and eviscerated body weights, as functions of BL, exceed 3.0 in Pacific herring from Auke Bay, and probably in Atlantic herring as well because of their similar morphology. Weight of mature gonads also have a greater-than-cubic relationship to BL in Auke Bay herring (the exponent was 4.4 for testes; the exponent of 3.9 for ovaries was within the range for ovaries in Atlantic herring).

The annual product (eviscerated body weight and gonad weight) is constantly proportional to BL through ages 2-6 and also through ages 8-12 in Pacific herring from Auke Bay, but the proportion is considerably lower in the 8-12 group. However, despite the two levels of production relative to BL, annual production corresponds more closely to BL than to eviscerated weight. Annual production may be lower relative to BL in the older group because suitable foods for adults may not be abundant in the Auke Bay vicinity. Most annual production in young Auke Bay herring goes into growth of eviscerated body weight. After age 6, production of sex products predominates, and by age 12, sex products compose over 90% of annual production.

Pacific herring probably develop genetic stocks that are distinguished by locale, spawning time, and cycles of gonad maturity and fat utilization in the females. The stocks probably are distinguished also by growth rate, age, or size at growth inflection and by partitioning of annual product between eviscerated body weight and gonads.

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CONTRIBUTIONS TO THE LIFE HISTORY OF BLACK SEA BASS, *CENTROPRISTIS STRIATA*, OFF THE SOUTHEASTERN UNITED STATES[1]

CHARLES A. WENNER, WILLIAM A. ROUMILLAT, AND C. WAYNE WALTZ[2]

ABSTRACT

Ages of black sea bass, *Centropristis striata*, from the South Atlantic Bight were determined from otoliths. Analysis of marginal increments showed that annulus formation occurred in April and May. The von Bertalanffy growth equation derived from back-calculated mean standard lengths at age was $lt = 341 (1 - e^{-0.2309(t+0.3010)})$, where t is age in years and lt = standard length at age. The oldest fish was age 10.

Centropristis striata is a protogynous hermaphrodite that undergoes sex succession at ages 1 through 8. The process of sex succession is described from histological examination of the gonads. The major spawning period is from March to May, and a minor spawn occurs in September-October. Mature males and females were encountered at age 1. Fecundity estimates ranged from 17,000 in a 108 mm SL female to 1,050,000 in a 438 mm SL fish, and were significantly related to length, weight, and age.

The instantaneous rate of total mortality of *C. striata* from catch curve analysis, ranged from 0.721 in 1978 to 1.320 in 1981 for commercial fish traps and 0.726 in 1979 to 1.430 in 1981 for hook-and-line gear. Petersen mark-recapture techniques were used to determine the population size of *C. striata* on two shallow-water patch reefs. Conversions of these estimates to densities gave 14-125 individuals per hectare.

The black sea bass, *Centropristis striata* (Linnaeus), is an important recreational and commercial serranid (Huntsman 1976; Musick and Mercer 1977; Low 1981) that occurs along the east coast of the United States from Massachusetts to Florida, with occasional individuals as far south as the Florida Keys (Fischer 1978). Within this range, *C. striata* is thought to form two populations separated at Cape Hatteras (Mercer 1978). The northern population migrates seasonally from shallow waters along the Middle Atlantic and southern New England coasts during summer to deeper water in the southern part of the Middle Atlantic Bight during the winter (Musick and Mercer 1977). Black sea bass in the Middle Atlantic Bight are harvested commercially with traps in shallow water during summer and with otter trawl gear when aggregated in deeper water in winter (Frame and Pearce 1973). Commercial catches are almost exclusively from traps in that part of the South Atlantic Bight from Cape Fear, NC to Cape Canaveral, FL where fishing is largely confined to patch reefs (live bottom habitat of Struhsaker 1969 or inshore sponge-coral habitat of Powles and Barans 1980) at depths from 20 to 46 m. South Carolina commercial landings were as high as 350.7 metric tons (t) in 1970, but show large annual fluctuations (Fig. 1).

Both the northern and southern populations have been aged by analyzing otoliths (Mercer 1978), with nine age groups identified north of Cape Hatteras and eight along the southeastern U.S. coast. However, sampling techniques could have biased the findings on southern *C. striata* since fishes came from commercial catches which are frequently culled at sea (Mercer 1978).

Black sea bass are protogynous hermaphrodites (Lavenda 1949), wherein most individuals function first as a female and later as a male. Most females mature by age 2; older age classes are composed predominately of male fish although sexually active males are in all age groups. Sexual succession occurs at ages 1 through 5 (Mercer 1978). The northern population spawns from June to October with peak reproduction in July and August off Virginia (Mercer 1978).

There is insufficient published information to describe the life history of this valuable commercial and recreational species in the South Atlantic Bight in detail. This report describes aspects of the life history of *C. striata* from the South Atlantic Bight, including age and growth, sex ratios, size and age

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[1] Contribution No. 205 from the South Carolina Marine Resources Center, Marine Resources Research Institute.

[2] Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

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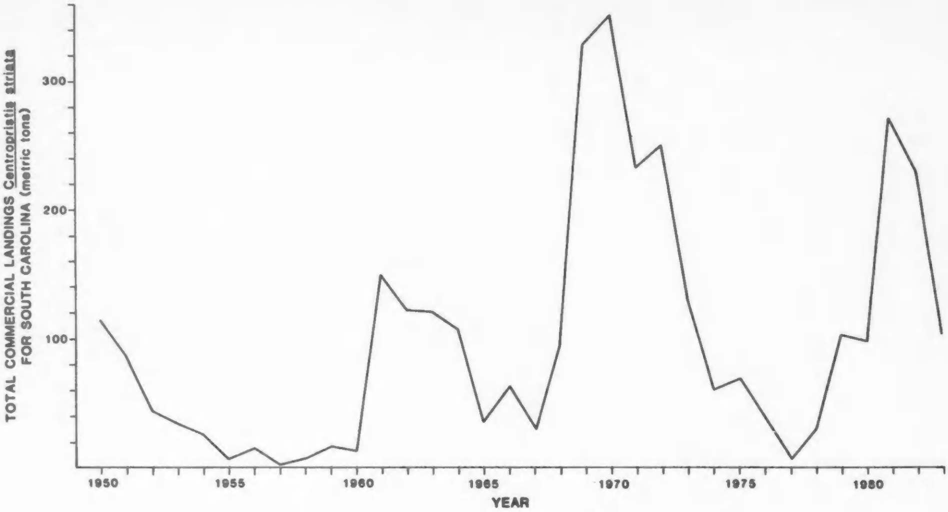

FIGURE 1.—Annual commercial landings of *Centropristis striata* in South Carolina.

at maturity and sexual succession, and fecundity. Additional information includes Petersen mark-recapture estimates of standing crop on reefs, and trends in the size and age composition with increased exploitation.

MATERIALS AND METHODS

Age and Growth

Most specimens were taken from the inshore sponge-coral habitat between lat. 31.5° and 33.5°N by commercial black sea bass traps (Rivers 1966), Antillean-S traps (Powles and Barans 1980), handlines, and trawl surveys from June 1978 through September 1981. Supplemental specimens were obtained from South Carolina commercial landings and other research programs to determine seasonal gonadal condition and time of annulus formation.

Centropristis striata were weighed to the nearest g and total (TL) and standard (SL) lengths were recorded to the nearest mm. Sagittae were removed and stored dry in envelopes for subsequent age determination. Unless damaged, the left sagitta was placed concave side up in a dish of water over a dark field and viewed at 12× magnification using a binocular microscope. When viewed with reflected light, sagittae displayed a central opaque field surrounded by alternating translucent and opaque bands. The central field varied in size and shape from a small opaque nucleus to a large opaque zone consisting of one or more broken rings (Fig. 2A, B). Since apparent daily growth rings have been observed on both the sagitta and lapillus of *C. striata* (Johnson[3]), this zone was interpreted by counting rings from the primordium to the edge of the central field. Otoliths were finely ground on both sides until the central area of apparent daily rings could be observed (Fig. 3A, B). They were then viewed with transmitted light on a compound microscope at 500× and/or 1,000× magnification.

The intercept of the otolith radius-SL relationship was used to derive mean back-calculated size at age by the Fraser-Lee method (Poole 1961; Carlander 1982). The von Bertalanffy growth equation (Bertalanffy 1938) was fitted to mean back-calculated SL at age using the SAS NLIN procedure (Helwig and Council 1979) employing Marquardt's algorithm and the SAS NLIN weight statement; mean back-calculated lengths were weighted by the reciprocal of the standard error of the mean squared. Both standard least squares linear regression (Sokal and Rohlf 1981) and geometric mean (GM) functional regression analyses were used to describe the relationship of length to length and length to weight.

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[3] G. David Johnson, Fish Division, U.S. National Museum, Washington, D.C. 20560, pers. commun. April 1982.

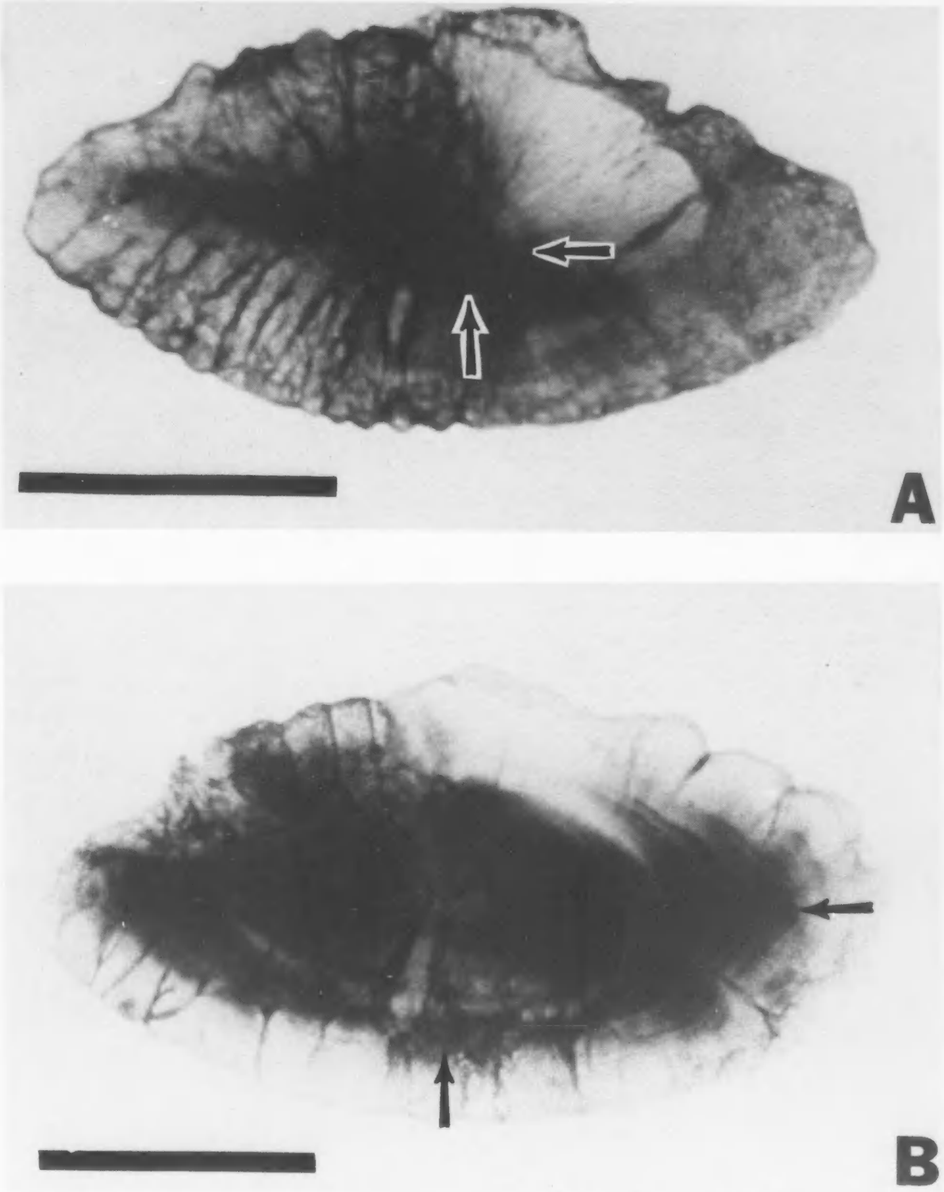

FIGURE 2.—Photomicrograph (16×) of the left sagittae from young-of-the-year *Centropristis striata*. A) Otolith with a small central nucleus (between arrows). B) Otolith with a large central zone consisting of a few broken rings (between arrows). Bars equal 1 mm.

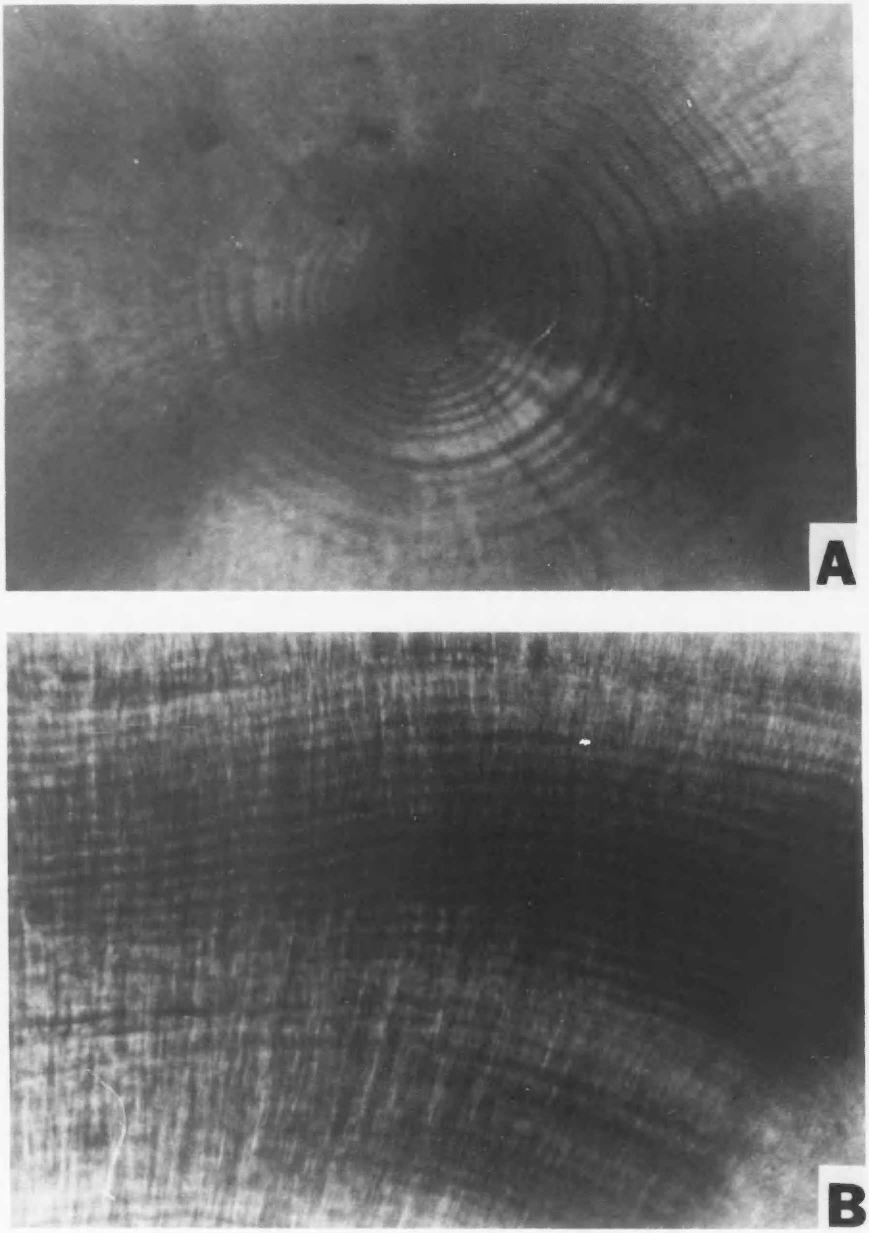

FIGURE 3.—Photomicrograph of sagittae from young-of-the-year *Centropristis striata*. A) Central primordium of the opaque nucleus showing growth rings for fish #1, Table 2; 400× magnification. B) Area of otolith near the edge of the central zone showing growth rings of fish #8, Table 2; 250× magnification.

Reproduction

Reproductive organs from 6,685 *C. striata* were resected at sea and fixed in formol-alcohol solution (Humason 1972) or 10% seawater Formalin[4]. After 2-6 wk fixation, the tissues were transferred to 50% isopropanol, processed through an Auto-Technican 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Sections (7 μm) were cut from each gonad by a rotary microtome, stained with Harris hematoxylin, and counter-stained with eosin-y. Histological sections from 300 fishes were read by two observers to develop agreement on sex and maturity stages; the remaining sections were then examined by a single observer. Sex and maturity stages (Table 1) which provided an accurate and objective estimate of reproductive status were modified from Smith (1965), Hilge (1977), and Mercer (1978) to determine size and age at first maturity, spawning season, and sex composition. The stage of gametogenesis and terminology used in gonadal descriptions follow Smith (1965), Combs (1969), Hyder (1969), Moe (1969), Mercer (1978), and Wallace and Selman (1981).

We included as males not only individuals whose gonads consisted entirely of testicular tissue but also those with functional testicular tissue (as judged by active spermatogenesis) as well as traces of inactive ovarian tissue. Females were defined as either having entirely ovarian gonads or inactive testicular tissue in a functional ovary. Transitional gonads included only those with obviously proliferating testicular tissue within a nonactive, regressing ovary. Simultaneous gonads were those combining equally developed male and female tissue. Immature bisexual gonads were designated as simultaneous juveniles to avoid any implication as to their function at maturity.

TABLE 1.—Histological criteria used in determining gonadal condition of black sea bass, *Centropristis striata*.

Gonad class	Testicular state	Ovarian state
Immature	Little or no spermatocyte development.	Small (<100 μm) basophilic oocytes.
Developing	A few primary and secondary spermatocytes through lumina filled with spermatozoa.	Predominance of oocytes with yolk vesicle formation through late vitellogenesis.
Ripe (running)	Predominance of spermatozoa, little active spermatogenesis.	Late vitellogenesis and presence of hydrated oocytes.
Spent	No spermatogenic activity, some residual sperm present in tubules.	Unspawned, mature oocytes undergoing atresia.
Resting	Some mitotic regeneration of spermatogonia and interstitial tissues.	Predominance of small basophilic oocytes with residual traces of atresia.
Transitional	—	Inactive or regressing ovarian tissue with concurrent testicular proliferation.

We successfully sexed 80-90% of the fish sampled by histological examination every month but April. More than 75% of those sampled in April were sexed by gross examination of the gonads, and although our determinations of the functional sexes of these gonads were probably correct, the relative occurrence of transitional and simultaneous gonads in April samples remains unclear. These data were thus used only to complete the seasonal frequencies of functional sexes.

Gonads from 115 maturing females collected during April 1979 were removed at sea, split open with a longitudinal incision, and placed in Gilson's solution (Bagenal 1967). Separated oocytes were washed and stored in 70% isopropyl alcohol after digestion of the ovarian tunic and connective tissue and then were decanted into a separatory funnel and diluted to 1 L for enumeration. Three to five 1 mL subsamples were removed from the suspension, which was well mixed by continuous aeration through the bottom of the funnel. Each subsample was transferred to a petri dish and counted at a magnification of 10×. Only ova >0.15 mm in diameter were counted since histological examination of the gonads of maturing and spent females showed only oocytes >0.15 mm developed during the spawning season. Total fecundity was estimated by expanding the mean of the subsamples to the total sample volume. Total fecundity was related to length and weight by standard least squares linear regression (Sokol and Rohlf 1981) and GM functional regression (Ricker 1973).

Mortality Estimates

Plots of $\log_e$ frequency on age indicated that black sea bass are fully recruited to commercial traps and hook-and-line gear at age 4, so mortality analysis applies to age 4 and older. The instantaneous rate of total mortality (Z) was estimated by standard least squares regression (Sokol and Rohlf 1981) from the slope of the right descending limb of the catch curve (Ricker 1975). Values of Z were also obtained by converting (appendix I in Ricker 1975) rates of survival (S) derived by Heinke, and Chapman and Robson estimates (Everhart and

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Youngs 1981). Not all fish collected were aged, so fish of known age were grouped into 1 cm length intervals by gear type for each survey to calculate percentages of each age in each size interval. These percentages were applied to the number of *C. striata* in each length interval to estimate age composition for the unaged fish (Ricker 1975).

Population Estimates at Specific Reef Sites

Petersen mark-recapture experiments were conducted at site 1 (lat. 32°30.3′N, long. 79°41.9′W; depth = 20 m; area ≅ 160 ha) during the summer of 1981 to estimate the population size of *C. striata* on this reef. In the summers of 1982 and 1983, we studied a second reef also (site 2: lat. 32°28.3′N, long. 78°14.5′W; depth = 23 m; area ≅ 120 ha). These reef areas were defined by the presence of attached algae and invertebrate growth (porifera, corals, echinoderms, bryozoans, anthozoans, and ascidians) as observed with a HYDRO products TC-125-5DA low-light-level underwater television camera during transects across the sites (for more details, see Wenner 1983). Study areas were mapped with an EPSCO C-Plot II LORAN-C plotter interphased with a SITEX 707 LORAN-C receiver.

Black sea bass were captured and recaptured at each site with commercial traps (Rivers 1966) and Florida snapper traps (0.9 m wide × 1.2 m long × 0.6 m high) fished for 45-90 min with cut clupeid bait (*Brevoortia tyrannus* and *Alosa aestivalis*). Black sea bass >20 cm TL, the approximate size of full retention in the traps, were measured to the nearest mm TL and tagged with 13 mm diameter plastic disc tags attached under the first dorsal fin with a nickel pin trimmed to the proper length and held in place with a 13 mm diameter plastic backing disc. Expansion of the swim bladder, due to reduced hydrostatic pressure, caused captured fish to float, so gas was released from the swim bladder with a 20-gauge hypodermic needle to enable fish to return to the bottom. For each experiment, 50-75 tagged fish, handled in the same fashion as those released, were held on the bottom in wire cages for about 24 h to determine tag-related mortality. Tagged fish were released over the reef, and sampling for recaptures started 24 h after tagging began. Experiments were completed in 48 h except at site 2 during the summer of 1982 when tagging was interrupted for 48 h by weather.

Preliminary estimates of population size are needed to determine sample sizes required for precise Petersen estimates (Everhart and Youngs 1981). Powles and Barans (1980) estimated the mean density of *C. striata* on reefs was 51 fish/ha from underwater television transects; expansion to the areas of our study sites gave preliminary estimates of 8,160 *C. striata* on site 1 and 6,120 on site 2. At site 1 we needed to tag 1,000 fish and examine 550 for tags to have an error no greater than 25% for 19 times out of 20 ($1 - \alpha = 0.95$ and $P = 0.25$). At site 2, we needed to tag 1,000 fish and examine 500. We used the adjusted Petersen estimate (Ricker 1975, p. 78):

$$N^* = \frac{(M + 1)(C + 1)}{(R + 1)}$$

where N^* = estimated population size
M = number of fish tagged
C = sample taken for census
R = number of tags returned in the sample taken for census.

The biomass of *C. striata* for each year and site was estimated as

$$\text{Biomass} = \sum_{1}^{a}\left(\frac{n^1}{n} \times PE \times g\right)$$

where n^1 = number of tagged fish in each 1 cm TL interval
n = total number of tagged fish
PE = population size from the Petersen estimate
g = weight in grams for the midpoint of each 1 cm TL size interval derived from the total length-weight relationship
a = number of 1 cm TL intervals of tagged fish.

In addition, the upper and lower confidence limits were substituted for *PE* in the above expression for estimates of the biomass at those population sizes.

RESULTS

Age and Growth

We believe that the central opaque zone of the sagitta may represent the first 1-4 mo of life in *C. striata*. This zone varied in length from 1.16 to 3.60 mm in the anteroposterior plane and from 0.56 to 1.54 mm in the dorsoventral plane (Fig. 4). We were not always able to make counts along a continuous

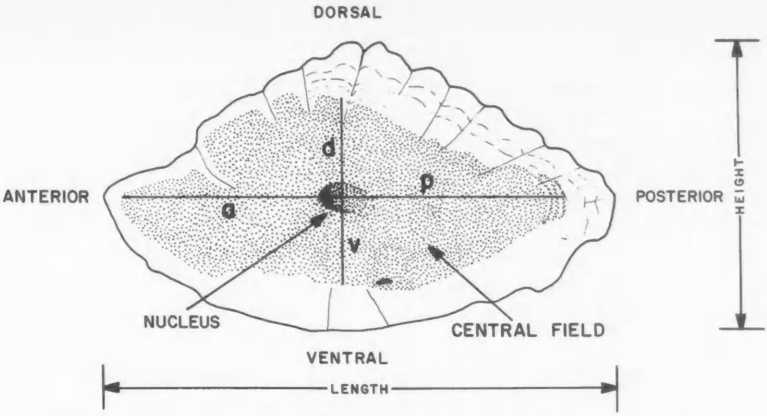

FIGURE 4.—Schematic representation of the left sagitta in young of the year *Centropristis striata* showing the orientation and direction of growth ring-counts in the central opaque zone. a = anterior, d = dorsal, p = posterior, v = ventral.

line because grinding did not expose all rings equally in the central zone. Also, in some instances, counting was halted at a distinct mark, such as a ring more distinctive than others, and we followed this mark around the sagitta to a site where rings were again visible and resumed counting. The number of rings in the central zone varied because of the otolith asymmetry and with the direction of the count (Table 2). For example, we obtained the following counts from the central primordium in one specimen (number 9 of Table 2): 90 rings to the dorsal edge of the central field (d of Fig. 4); 95 rings to the ventral edge (v of Fig. 4); 129 rings to the posterior edge (p of Fig. 4).

Since marginal increments on the otoliths should approach zero during the time of annulus formation, we calculated their monthly means to determine if one opaque band was laid down during each year on the sagittae of *C. striata*. Generally, a single annulus was formed during April and May in all age groups (Fig. 5). We found that the ring was deposited unevenly around the sagitta, with the dorsal margin of the annulus being the last to be completed.

We identified 10 age groups in the South Atlantic Bight population of *C. striata*, which exceeded the previous reports of 7 (Cupka et al. 1973[5]) and 8 (Mercer 1978) groups. Observed mean lengths and weights increased with age; however, small sample sizes in ages 8 through 10 masked this trend (Table 3). Regressions of weight on length (TL and SL) and length on length are in Table 4.

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[5] Cupka, D. M., R. K. Dias, and J. Tucker. 1973. Biology of black sea bass, *Centropristis striata* from South Carolina waters. Unpubl. manuscr. South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

TABLE 2.—Data from *Centropristis striata* examined for daily growth rings. Refer to Figure 2 for otolith morphology and terms (d, v, p, and a) used in the counts. Numbers in parentheses are ranges of several counts; dashes indicate no counts made.

	Fish			Otolith		Central field					
								Daily ring counts			
No.	TL (mm)	SL (mm)	WT (g)	Height (mm)	Length (mm)	Height (mm)	Length (mm)	d	v	p	a
1	66	54	4	1.56	broken	0.92	1.76	—	—	(84-89)	—
2	60	48	2	1.52	3.08	0.56	1.16	28	(25-26)	(50-51)	—
3	95	74	11	2.24	4.44	1.54	3.25	—	(109-120)	—	—
4	125	98	30	2.92	4.88	1.54	3.60	—	135	—	—
5	78	61	4	1.82	broken	0.98	broken	105	—	—	—
6	76	58	5	1.84	3.44	1.08	2.68	106	—	121	—
7	78	60	4	1.78	3.40	1.12	2.88	(98-106)	—	—	—
8	81	63	5	1.92	3.60	1.52	3.40	51	—	—	81
9	—	64	6	1.84	3.52	1.16	3.08	90	95	—	129

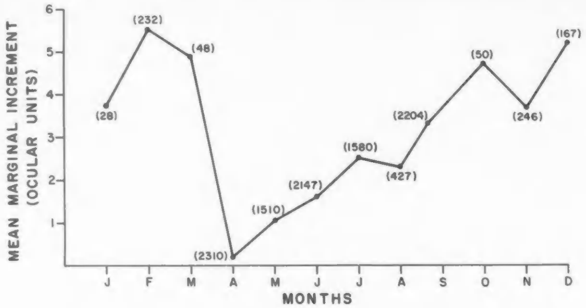

FIGURE 5.—Mean marginal increment by month for otoliths of *Centropristis striata*. Number in parentheses represent monthly number of otoliths examined.

TABLE 3.—Means ($\bar{x}$), standard deviations and sample sizes for observed lengths (mm) and weights (g) by age for *Centropristis striata*.

	Total length			Standard length			Weight		
Age	*n*	($\bar{x}$)	SD	*n*	($\bar{x}$)	SD	*n*	($\bar{x}$)	SD
0	185	94	25	186	73	20	186	17	16
1	818	163	27	830	127	21	822	70	38
2	2,712	215	28	2,714	167	21	2,688	152	65
3	4,271	249	34	4,263	192	24	4,246	228	102
4	2,376	291	40	2,371	222	28	2,350	348	142
5	951	337	46	950	256	32	904	520	206
6	497	375	48	497	284	35	460	711	266
7	138	395	50	139	299	38	121	823	280
8	48	394	50	48	301	38	43	838	289
9	10	406	58	10	305	46	7	816	383
10	4	404	45	4	303	35	3	685	85

TABLE 4.—Least square linear and geometric mean functional regression equations of weight (WT) on total length (TL) and standard length (SL), and length-length for *Centropristis striata*. Weight units are grams and lengths are millimeters. All least squares regressions were significant at $\alpha = 0.01$.

Least squares equation	*n*	r^2	GM functional equation
$\log_{10} WT = -4.375 + 2.800 \log_{10} TL$	12,281	0.97	$\log_{10} WT = -4.478 + 2.844 \log_{10} TL$
$\log_{10} WT = -4.328 + 2.978 \log_{10} SL$	12,284	0.98	$\log_{10} WT = -4.398 + 2.949 \log_{10} SL$
$TL = -9 + 1.4\ SL$	12,473	0.97	$TL = -12 + 1.4\ SL$
$SL = 12 + 0.7\ TL$	12,473	0.97	$SL = 9 + 0.7\ TL$

Least squares regressions of SL (mm) on otolith radius (OR in ocular units) are

$$\log_{10} SL = 0.668 + 1.056 \log_{10} OR;$$

$$n = 12,011;\ r^2 = 0.89.$$

The intercept of the SL-OR relationship was used to obtain the mean back-calculated SL's at age which were lower than observed SL's in all cases (Table 5). Weighted least square estimates of von Bertalanffy parameters, asymptotic 95% confidence

TABLE 5.—Observed and back-calculated mean standard length in mm and von Bertalanffy standard length at age for *Centropristis striata*.

Age	*n*	Observed SL	Back-calculated SL	von Bertalanffy SL
1	830	127	88	88
2	2,714	167	142	141
3	4,263	192	180	182
4	2,371	222	212	215
5	950	256	244	241
6	496	284	271	261
7	139	299	283	278
8	48	301	289	291
9	10	305	296	301
10	4	303	303	309

limits and asymptotic standard errors were also derived from these data (Table 6). Estimates of an average asymptotic size (L_∞) depended not only on the number of age groups present and the distribution of individuals within each group, but also on the curvature of the age-size relationship. An average asymptotic size of 341 mm SL appeared conservative. The largest fish aged was 390 mm SL and only 0.6% of all *C. striata* sampled were larger than 341 mm SL. The largest specimen caught off the South Carolina coast was estimated to be about 490 mm SL (S.C. Wildlife and Marine Resources Department[6]). Comparisons of von Bertalanffy back-calculated and observed SL at age are in Table 5.

TABLE 6.—Estimated von Bertalanffy parameters describing the growth of *Centropristis striata*. The weighted residual sums of squares = 238.46. SE = standard error; C.L. = confidence limits.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% C.L.	
			lower	upper
L_∞	341	17.818	298	383
k	0.2309	0.0221	0.1787	0.2831
t_0	−0.3010	0.0560	−0.4335	−0.1685

Reproduction

The generalized ovarian structure of *C. striata* is similar to that of *Epinephelus fulva* (Smith 1965), *E. morio* (Moe 1969), and *Hemanthias vivanus* (Hastings 1981). The bilobed organ is suspended by mesenteries from the swim bladder in the posterior region of the body cavity. The lobes fuse posteriad, and their lumina form a common oviduct. Blood vessels and nerves enter the ovary at the anterior point of each lobe's suspension and continue posteriad medial to the supportive mesenteries along the dorsomedial surface of each lobe. The lumina are lined with folded germinal epithelium (ovarian lamellae), within which oocytes develop and mature. The lamellae are first seen protruding from the dorsal region of the lumen at the boundary of the ovary and the alamellar oviduct. They continue along both sides of the lumen in the area of gonadal confluence until only the ventralmost region of the ovary is alamellar. This alamellar area is confluent with the oviduct and extends anteriad to half of the lengths of each ovarian lobe (Fig. 6A). The alamellar regions of female gonads were bordered throughout their extent by testicular precursor cells (Figs. 6A, B; 7A). Although these bands of cells were found in varying stages of development in all ovarian tissues, the most active proliferation of identifiable spermatogenic tissue (as manifested by transitional gonads; Table 7) occurred after the spring and fall spawning seasons (described later). Both increased ovarian inactivity and degeneration coincided with the proliferation of testicular tissue during sexual succession (simultaneous hermaphroditic development is treated below). No instance of active ovarian development concurrent with testicular degeneration was observed.

Sexual transition commenced in the posterior region of the ovary with the expansion of testicular lobes into the ovarian lumen. This proliferation proceeds anteriad, with sperm sinus forming in the ovarian tunic adjacent to the testes. Testicular growth appears to be the result of mitotic spermatogonial development, although limited spermatogenic processes, including spermatozoa formation, are not uncommon (Fig. 7B). The sperm sinuses, as well as the vas deferens (which form within the oviductal wall) apparently result from ruptures in their respective surrounding tissues, as suggested by Hastings (1981), because there was no cell lining associated with these structures (Fig. 7B).

Simultaneously developed hermaphroditic gonads were found in all maturity stages. However, only 3% of the fishes exhibited this phenomenon, and we were unable to determine if the vas deferens had an external opening; therefore, we lack definitive proof that these fish were functional simultaneous hermaphrodites.

Histological sections of immature ovaries contained only oogonia and small basophilic, previtellogenic oocytes about 8-100 μm in diameter. Maturing ovaries had oocytes 100-500 μm in diameter, in

TABLE 7.—Monthly sex composition data for *Centropristis striata* along with χ^2 values for tests of a 1:1 sex ratio. ** = $P < 0.01$, 1 df; * = $P < 0.05$, 1 df.

Month	Males	Females	Transitional	Transitional (%)	♂:♀	χ^2
January	13	13	1	3.7	1:1	—
February	111	107	8	3.6	1:0.96	0.07
March	15	7	0	0	1:0.47	2.91
April	928	1,685	122	4.5	1:1.82	219.30**
May	404	497	145	13.9	1:1.23	9.60**
June	509	1,039	383	19.8	1:2.04	181.46**
July	132	368	84	14.4	1:2.79	111.39**
August	112	246	42	10.5	1:2.20	50.16**
September	668	1,109	262	12.8	1:1.66	109.44**
October	35	17	1	1.9	1:2.05	5.12*
November	64	150	27	11.2	1:2.34	34.56**
December	34	19	13	19.7	1:0.56	4.45

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[6] Office of Conservation, Management, Marketing and Recreational Fisheries, S.C. Wildlife and Marine Resources Department. 1982. South Carolina Saltwater Sport Fishing Tournaments and State Record Fish. S.C. Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412.

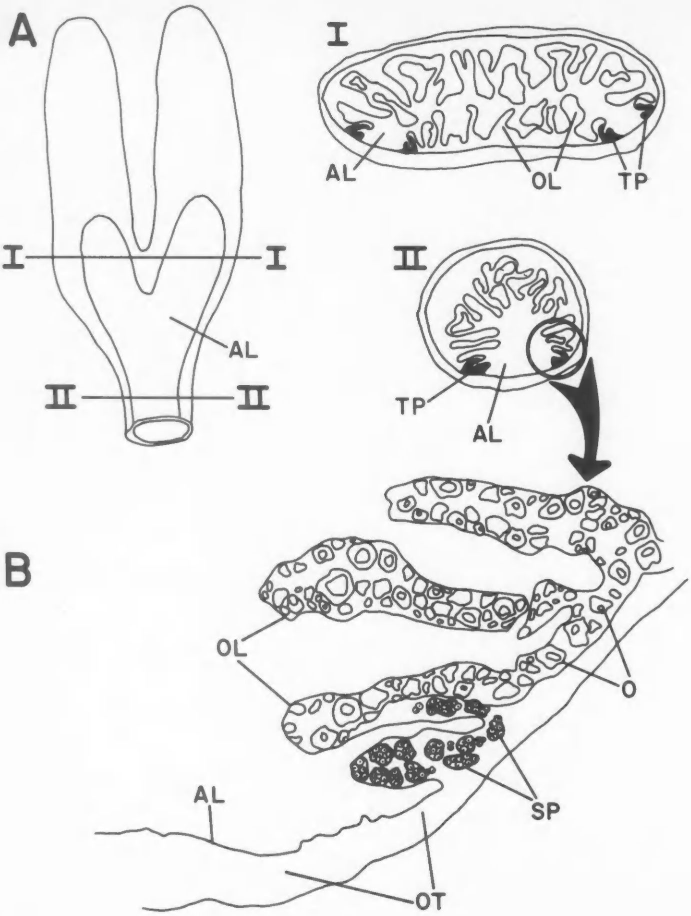
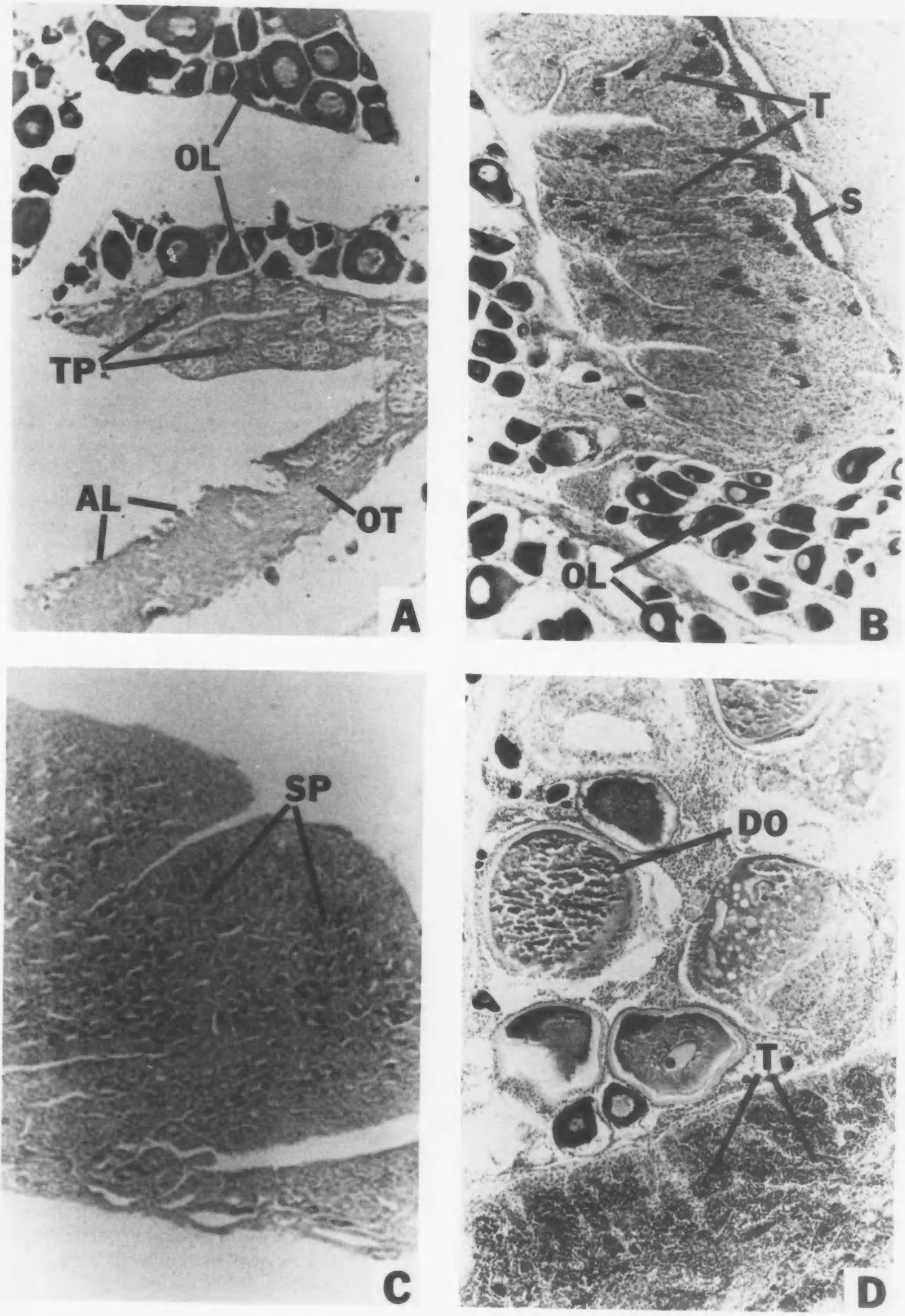


FIGURE 6.—Schematic representation of a functionally female ovary from *Centropristis striata.* A) Ventral view of ovary showing the alamellar region. Cross sections of the ovary were made in planes I-I and II-II, and show the positioning of the primordial testicular tissue at the boundary of the alamellar regions. B) An enlargement of the area indicated, showing the cellular relationships of the alamellar area, testicular primordia and ovarian lamellae. AL = alamellar region, O = oocytes, OL = ovarian lamellae, OT = ovarian tunic, SP = chords of spermatogonia, TP = testicular primordia.

FIGURE 7.—Photomicrographs of histological sections of gonads from *Centropristis striata.* A) Cross section taken from the posterior region of a functional ovary showing the alamellar region and testicular primordia, 250× magnification. B) Cross section taken from the posterior region of a gonad undergoing transition, 250× magnification. C) Cross section of immature testicular tissue from a 133 mm SL fish, 100× magnification. D) Cross section of a simultaneous gonad showing active testicular and ovarian development, 100× magnification. AL = alamellar region, DO = developing oocyte, OL = ovarian lamellae, OT = ovarian tunic, S = spermatozoa, SP = spermatogonia, T = testicular tissue.


OL
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stages from yolk vesicle formation (Wallace and Selman 1981) through late vitellogenesis. Oocytes (500-740 μm in diameter) in ripe ovaries showed coalescence of yolk globules and hydration. Gonads from spent and resting females contained decreasing amounts of unspawned, atretic oocytes and empty, ruptured follicles.

Gonads from immature males were characterized by primary and secondary spermatogonia (Fig. 7C), and isolated, more fully developed seminiferous crypts in some instances. In developing testes we saw several stages that included gonadal tissue composed mostly of primary and secondary spermatocytes, as well as sperm sinuses filled with mature spermatozoa. Ripe testes had sperm sinuses and ducts packed with spermatozoa; the remainder of the gonad showed only a little spermatogenesis. Spent testes showed both the lack of spermatogenic activity and the presence of large amounts of unshed sperm, whereas gonads in resting males showed mitotic proliferation of next season's spermatogonia and interstitial tissues.

Females comprised 52% of the sexed *C. striata* and were mature in ages 1 through 8. We found mature gonads in none of the females at age 0, 48.4% at age 1, 90.3% at age 2, 99.1% at age 3, and 100% at all older ages. Immature females were 50-180 mm SL, and the smallest mature specimen was 110 mm SL. Males made up 30.6% of the fishes sexed, and 1.3% of these males were immature and were in ages 0-1 with lengths of 50-180 mm SL. The smallest mature male was 100 mm SL.

Gonads of 14% of the *C. striata* examined histologically showed these fishes undergoing sex succession. These were found primarily after the major spawn (January-April), and during a brief period after the lesser spawn during September-October (Table 7). The smallest individuals exhibiting sex succession were in the 120-139 mm SL interval (Table 8); however, the greatest frequency of transitional gonads (77%) occurred in fishes 160-259 mm SL. Males made up 15.4% of the age 0 *C. striata* and 10.5% of fishes <120 mm SL (Tables 8, 9; Fig. 8). The relative abundance of males increased with both size and age, and fish containing transitional gonads increased in abundance during the period of the most rapid decline in the relative number of females (Fig. 8).

Both male and female tissue developed simultaneously in the same gonad in 3% of the *C. striata* examined histologically (Fig. 7D). This occurred in immature, developing, spent, and resting fishes. Both testicular and ovarian tissues showed equivalent maturity stages within the same gonad; that is, male and female germinal tissue developed concurrently.

The overall sex ratio for *C. striata* in the South Atlantic Bight was 1♂:1.71♀. We found significantly more females than males from April through November, and inconsistency in the ratio between December and March probably reflected both inadequate and biased samples from these months. Ratios were significantly different at all sizes from an hypothesized 1:1 (Table 8) except at 200-219 mm SL. The abundance of males begins to increase in that size group and also in age class 4 (Table 9) as the abundance of females declines, reflecting the increased frequency of the sex succession process.

Centropristis striata has a major spawn from January through April when 80-100% of the ovaries were developing or ripe (Fig. 9). Although a second period of ovarian activity was found in September, it was interpreted as being of a lesser nature since only 30% of the females were developing or ripe.

TABLE 8.—Sex composition and χ^2 values for tests of a 1:1 sex ratio of *Centropristis striata* by 20 mm SL intervals. ** = $P < 0.01$, 1 df; * = $P < 0.05$, 1 df.

SL	Males	Females	Transitional	Transitional (%)	♂:♀	χ^2
−119	16	136	0	0	1:8.50	94.74**
120-139	28	206	4	1.7	1:7.36	135.40**
140-159	74	525	46	7.1	1:7.10	339.57**
160-179	170	1,145	200	13.2	1:6.74	722.91**
180-199	301	796	289	20.8	1:2.64	223.36**
200-219	347	423	112	15.3	1:1.22	7.50*
220-239	335	185	94	14.8	1:0.55	43.27**
240-259	278	106	67	13.0	1:0.38	77.04**
260-279	179	41	33	4.2	1:0.23	86.56**
280-299	154	26	8	2.5	1:0.17	91.02**
300-319	111	5	3	3.3	1:0.04	96.86**
320-339	57	1	2	3.5	1:0.02	54.07**
>339	55	0	2	3.6		
Total	2,105	3,595			1:1.70	

TABLE 9.—Sex composition and χ^2 values for tests of a 1:1 sex ratio of *Centropristis striata* by age. ** = $P < 0.01$, 1 df.

Age	Males	Females	Transitional	Transitional (%)	♂:♀	χ^2
0	10	55	0	0	1:5.50	31.2**
1	42	315	20	5.3	1:7.50	208.8**
2	251	1,066	185	12.3	1:4.20	504.3**
3	561	1,449	447	18.2	1:2.60	392.3**
4	635	479	223	16.7	1:0.75	21.8**
5	274	84	59	5.0	1:0.31	100.8**
6	189	17	8	3.7	1:0.09	143.6**
7	54	2	2	3.4	1:0.04	48.3**
8	13	0	0	0		
9	2	0	0	0		
10	2	0	0	0		

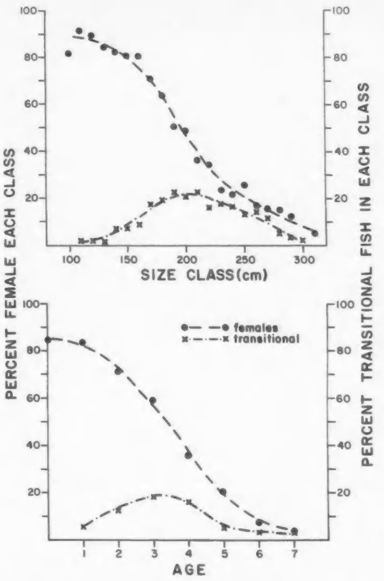

FIGURE 8.—Percent female and transitional *Centropristis striata* by size and age.

Fall spawning probably extended into October because many fishes obtained in November had recently spent ovaries.

Fecundity was significantly related to SL, TL, weight, and age with the former three equations having by far the highest r^2 values (Table 10). The least squares linear regression model of fecundity on age explained only 33% of the variation in fecundity. Observed mean fecundity and its standard error increased with age (Table 11). The lowest observed fecundity (17,000) was in a 2-yr-old fish (SL = 108 mm; TL = 140 mm; weight = 45 g) and the largest (1,050,000) was in a 438 mm SL fish (TL = 454; weight = 1,371 g) of undetermined age.

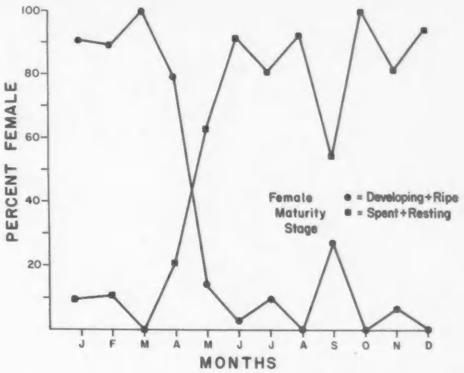

FIGURE 9.—Maturity stages of female *Centropristis striata* by month to illustrate bimodal spawning.

Mortality

Instantaneous rates of total mortality, as derived from catch curves, for *C. striata* ranged from 0.721 to 1.430, and actual mortality rates were from 0.513 to 0.761. Values increased from 1978 to 1981. For example, values of A rose from 51.3 to 73.3% for trap-caught fish and from 51.6 to 76.1% for hook-and-line caught fish older than age 4 (Table 12). Mortality values of trap-caught and hook-and-line caught *C. striata* were similar within years for each estimation procedure. Mortality values, moreover were similar between estimation procedures. We found a significant correlation between the instantaneous

TABLE 10.—Least squares linear and geometric mean functional regression equations of fecundity (fec) on total length (TL), standard length (SL), weight (WT), and age for *Centropristis striata*. Weight units are grams and lengths are millimeters. All least squares regressions were significant at α = 0.01.

Least squares equation	n	r^2	GM functional equation
$\log_{10}$ fec = −0.605 + 2.335 ($\log_{10}$ TL)	115	0.62	$\log_{10}$ fec = −2.098 + 2.959 ($\log_{10}$ TL)
$\log_{10}$ fec = −0.309 + 2.318 ($\log_{10}$ SL)	115	0.65	$\log_{10}$ fec = −1.589 + 2.879 ($\log_{10}$ SL)
$\log_{10}$ fec = 3.057 + 0.822 ($\log_{10}$ WT)	115	0.65	$\log_{10}$ fec = 2.587 + 1.022 ($\log_{10}$ WT)
$\log_{10}$ fec = 4.529 + 0.913 ($\log_{10}$ Age)	110	0.33	$\log_{10}$ fec = 4.196 + 1.580 ($\log_{10}$ Age)

TABLE 11.—Observed mean fecundity at age and its standard error ($S_{\bar{x}}$) for *Centropristis striata*, in the South Atlantic Bight.

Age	Mean fecundity	$S_{\bar{x}}$	n
2	61,846	8,089	13
3	94,801	4,406	55
4	115,411	8,900	27
5	160,000	50,720	7
6	226,040	46,706	5
7	287,350	80,650	2
8	137,400	—	1

TABLE 12.—Instantaneous (Z) and actual (A) rates of total mortality for *Centropristis striata* in the South Atlantic Bight. Gear types: T = trap; H&L = hook and line.

		Catch curve		Heinke		Chapman-Robson		Means	
Year	Gear	Z	A	Z	A	Z	A	Z	A
1978	T	0.721	0.513	0.841	0.568	0.991	0.628	0.851	0.569
1979	T	0.906	0.595	0.819	0.559	0.872	0.582	0.866	0.579
1979	H&L	0.726	0.516	0.759	0.532	0.650	0.478	0.712	0.509
1980	T	1.030	0.643	1.020	0.639	1.181	0.693	1.077	0.658
1980	H&L	0.905	0.595	0.944	0.611	1.016	0.638	0.955	0.615
1981	T	1.320	0.733	1.347	0.740	1.328	0.735	1.332	0.736
1981	H&L	1.430	0.761	1.347	0.740	1.492	0.775	1.423	0.759
1982	T	1.279	0.722	1.382	0.749	1.443	0.764	1.368	0.745
1982	H&L	1.246	0.712	1.277	0.721	1.309	0.730	1.277	0.721

rate of total mortality from trap data and the South Carolina commercial landings from 1978 to 1982 (Fig. 10).

Population Estimates at Specific Sites

Mortality of *C. striata* attributable to tagging occurred only once, during the 1983 experiment of site 2 when 6% of the fishes (3 of 50) died during the holding period. Therefore, we reduced the number of tagged fish-at-large (M) by 6% to account for this tagging related mortality.

Between 1981 and 1983, a decline in the order of magnitude from 20,070 to 2,236 individuals (88.9%) occurred in the estimated abundance of *C. striata* at site 1. On this reef, the abundance declined 60.6% from 1981 to 1982 and another 75.5% from 1982 to 1983 (Table 13). Abundance at site 2 declined 52.9% between 1982 and 1983. Biomass of *C. striata* declined by an order of magnitude on site 1 from 4,836 kg in 1981 to 491 kg in 1983 (Table 13). This was an overall decrease of 89.9%. Site 2 had a 62% decline in biomass from 2,150 kg in 1982 to 810 kg in 1983. Our estimates are for fish >20 cm TL, the only ones vulnerable to the traps. Therefore, density and biomass estimates are minimum values.

In addition to the declines in population size and biomass of *C. striata*, there were decreases in mean size and age. Mean TL was 3 cm less in 1983 than in 1981 at site 1, whereas *C. striata* were on average 2 cm smaller in 1983 than 1982 at site 2. Not only were the means reduced, but also the frequency distribution became more skewed towards the smaller size intervals and the contributions of larger

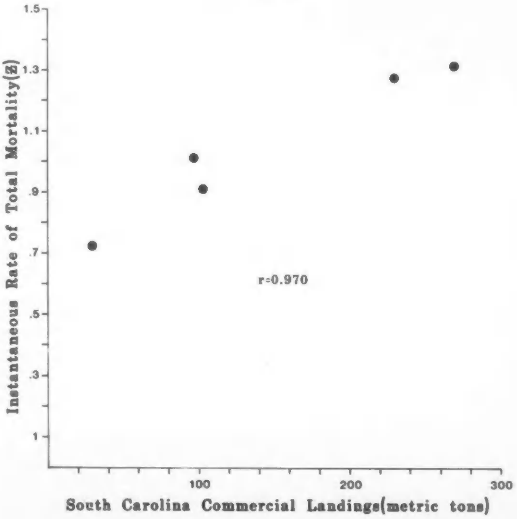

FIGURE 10.—Plot of the instantaneous rate of total mortality (Z) as determined from resource survey data (1978-81) and the South Carolina commercial landings of *Centropristis striata* for that year.

TABLE 13.—Summary of Petersen mark-recapture population estimates, biomass, and density (number and kg/ha) estimates for black sea bass, *Centropristis striata*, on two sponge-coral habitat sites. 95% confidence limits (C.L.) of $p(= R/C)$ were determined by the methods of Cochran (1977).

	Site 1			Site 2	
	1981	1982	1983	1982	1983
C	634	529	438	446	679
M	1,042	1,169	1,084	901	854
R	32	67	212	50	155
95% C.L. of R	21.9-44.2	53.4-83.1	193.2-230.8	33.9-57.5	135.1-175.2
p	0.50	0.127	0.484	0.112	0.228
95% C.L. of p	0.035-0.070	0.101-0.157	0.441-0.527	0.076-0.129	0.199-0.258
N^{*1}	20,070	9,119	2,236	7,906	3,727
95% C.L. of N^*	14,653-28,921	7,347-11,399	2,055-2,453	6,892-11,553	3,300-4,272
μ	0.032	0.058	0.196	0.056	0.182
95% C.L. of μ	0.022-0.043	0.046-0.072	0.179-0.213	0.039-0.065	0.159-0.206
Biomass (kg)	4,836	2,077	491	2,150	810
95% of biomass (kg)	3,530-6,959	1,673-2,595	451-539	1,874-3,142	717-928
Number/ha	125	57	14	66	31
95% C.L. of number/ha	92-181	46-71	13-15	57-96	28-36
kg/ha	30.2	13.0	3.1	17.9	6.7
95% C.L. of kg/ha	22.1-43.5	10.5-16.2	2.8-3.4	15.6-26.2	6.0-7.7

[1] Adjusted Petersen estimate (Ricker 1975).

fishes to the populations was greatly reduced (Fig. 11). Mean age declined 0.5 years at site 1, and the age composition shifted towards younger age classes (Fig. 12). Fishes age 4 and older went from 42% of the population in 1981 to 25% in 1982 and 9% in 1983.

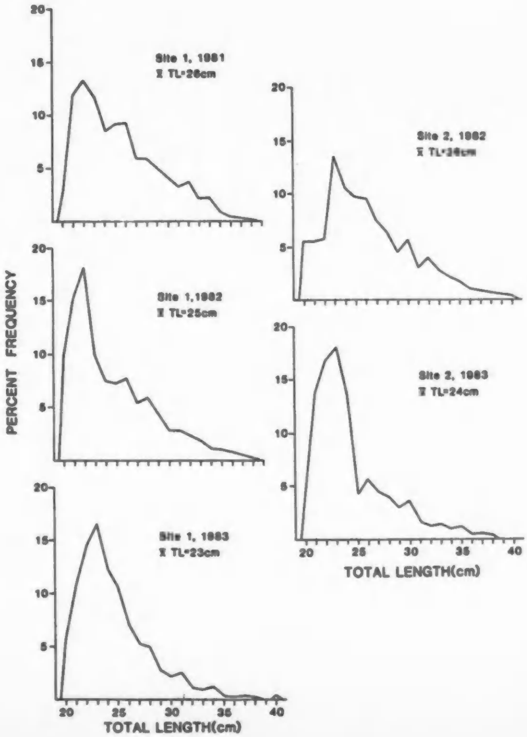

FIGURE 11.—Size-frequency distribution of *Centropristis striata* from five discrete mark-recapture tagging studies.

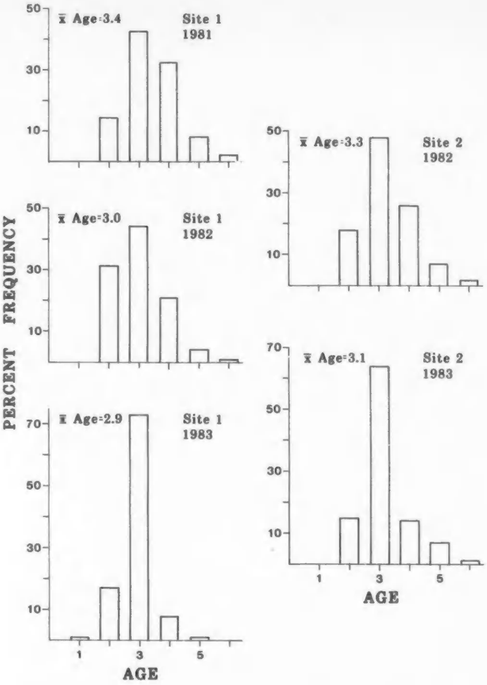

FIGURE 12.—Age composition of *Centropristis striata* at the two experimental mark-recapture sites.

DISCUSSION

Age and Growth

The cause of the variation in size and shape of the sagitta's central field in *C. striata* is unknown, however, differing size of the nuclei of Atlantic herring, *Clupea harengus*, can be related to spawning season (Postuma 1974). Further studies are needed to determine if these differences can be related to spawning time of *C. striata* in the South Atlantic Bight.

Inadequate validation in many studies that estimate age have been noted by Beamish and McFarlane (1983), and they have reemphasized the need for verification of aging technique. Our attempts at validation have shown that one annulus is formed each year during April-May. Also, our counts of presumed daily growth rings have provided circumstantial support for the formation of the first annulus. A similar approach was used by Radtke et al. (1985) in their study of the oyster toadfish, *Opsanus tau*.

Our mean back-calculated lengths agree well with Mercer's (1978) data for *C. striata* from the South Atlantic Bight up to age 5; however, ours are much smaller than Cupka et al. (fn. 5). Our lengths at age are consistently smaller than *C. striata* from the Middle Atlantic Bight (Mercer 1978). Mercer (1978) attributed size at age differences between the two areas to gear selectivity, yet our results suggest that *C. striata* from the South Atlantic Bight are smaller than those of the Middle Atlantic Bight. The larger size at age found by Cupka et al. (fn. 5) may reflect the population of *C. striata* in the South Atlantic Bight prior to heavy exploitation that began in 1969.

Since estimates of L_∞, K, and t_0 are affected by several nonbiological, methodical factors, direct comparisons of these growth parameters between different studies are of limited value. However, when viewed in relative terms, they can indicate general differences or similarities between studies, species, or areas. Our estimate of L_∞ (341 mm SL) was much closer to Mercer's (1978) value (L_∞ = 352 mm SL) than that of Cupka et al. (fn. 5) (625 mm SL). Our growth coefficient (K) was higher, indicating that *C. striata* achieves maximum attainable size more rapidly than previously reported. These differences could have been caused by sampling methodologies and/or conditions of the population of South Atlantic Bight *C. striata* at the time the studies were conducted.

Reproduction

Smith (1965) established a phylogeny of serranid fishes based on three types of hermaphroditism. Most primitive is the *Serranus*-type gonad found in *Serranus* and *Hypoplectus*, genera which are simultaneously hermaphroditic with male and female germinal tissues well separated by connective tissues. The middle type of this trio is the protogynously hermaphroditic *Rypticus-Anthias*-type gonad where testicular takeover commences with proliferation of preexisting spermatogonia located in crypts along the alamellar regions of the ovary and gametogenic tissues remain separated by connective tissue throughout sexual transition. Most advanced is the protogynous hermaphroditic *Epinephelus*-type gonad where testicular tissue cannot be found before sexual transition commences. During this process, crypts of spermatogonia differentiate and proliferate within the ovarian lamellae where they are intermixed with oogonia and oocytes.

Citing Lavenda (1949), Smith (1965) classified *C. striata* within the *Epinephelus*-type, an error corrected by Mercer's (1978) demonstration that morphological events during sexual transition in *C. striata* most resemble those of the *Rypticus-Anthias*-type gonad. Sexual succession in *C. striata* results from hypertrophy of bands of testicular primordia that lie along borders of the alamellar region of the ovary, not the proliferation of crypts of tissue that Mercer (1978; see also Smith 1965) reported. The arrangement of the primordial testicular ridges in *C. striata* is the same as in the protogynous *Hemanthias vivanus* (Hastings 1981).

The testicular primordia in *C. striata* is located in a similar region of the gonad as is the testicular portion of the simultaneously functioning gonad of *Serranus tigrinus* (Smith 1965). Though not stated by Smith (1965), the testes of *S. tigrinus* might border the alamellar region of the ovarian section as does the testicular primordial cells in *C. striata*, a gonadal similarity also noted between *H. vivanus* and *S. tigrinus* (Hastings 1981). No phylogenetic inferences should be drawn from these data, because gonadal development varies even among the closely related simultaneous hermaphrodites of the genera *Serranus* and *Diplectrum*. *Centropristis striata*, *H. vivanus*, and probably *R. maculatus* (see Smith 1965) have similar gonadal morphologies and strategies of sex succession, but these species are usually not considered closely related. Gonadal morphologies may one day be important in determining serranid phylogenetic relationships, but more observations of all serranids are necessary.

The simultaneously functioning gonad of *C. striata* has morphology similar to that of *Serranus* (Smith 1965) in which discrete areas of testicular tissue empty into peripherally located sinuses, and oocytes discharge centrally. Sperm sinuses within the wall of the simultaneous gonads are well developed in *C. striata*, but it is not known if they are functional, i.e., permit sperm to exit the body along with the oocytes.

We found sizes and ages of *C. striata* undergoing sex succession which were similar to those Mercer (1978) reported in the South Atlantic Bight; however, we found a much higher incidence of transitional fish. Since Mercer (1978) found only 4% of *C. striata* from this area were undergoing sex succession, she offered two mechanisms for her abundance (38%) of mature males: 1) development of mature males from both immature males and juvenile hermaphrodites was very important, or 2) the rate of sexual transition was very rapid in this species.

We feel that both of Mercer's arguments were at best incomplete because of her small sample sizes from the South Atlantic Bight. Since we found few immature males and juvenile hermaphrodites in our samples, the probability is low that mature males develop solely from these. Also, we acknowledge the presence of serranids which show rapid sex succession (Fishelson 1970; Fricke and Fricke 1977) and believe the low frequency of individuals undergoing sex succession seen in most Epinepheline groupers probably reflects a similarly short-lived process. However, the presence of *C. striata* undergoing sex succession throughout the year, and their occurrence at sizes where the frequency of females declines, leads us to conclude that the primary source of mature males is through sex succession from active females.

We found secondary testes (sensu Harrington 1971) in all male *C. striata* including immature specimens. This morphology is not unique to *C. striata*. Hastings (1981) observed no primary male *H. vivanus* and suggested they all passed through an initial female phase. This same secondary gonadal morphology occurs in the secondarily gonochoristic serranid *Paralabrax clathratus* (Smith and Young 1966), and Reinboth (1970) indicated all male serranids are derived from females.

Overall, sex ratios of *C. striata* were significantly different from an hypothesized 1♂:1♀ in favor of females. Females significantly outnumbered males up to an intermediate size and age, at which time the significantly different ratios favored males. Fishelson (1975) stated that sex ratios should approximate 1♂:1♀ at some stage if all protogynous females undergo sex succession. Given the alternating ratios of sexual abundance with size and age, and considering that no female older than age 7 and few larger than 330 mm SL were found in our samples, leads us to conclude that all *C. striata* have the potential to undergo sex succession.

Population Estimates

The underlying assumptions of the Petersen method for population estimates were met in this study. We found tag-related mortality in only one experiment and adjusted the number of fish marked for it. We feel all tags were accounted for and tag loss was minimal, because tags were firmly anchored to the fish and were bright orange. Tagged fish were not randomly distributed over the study site, but they were released during vessel drifts governed by wind and surface currents and may be effectively random. We assumed minimal immigration and emigration because our experiments covered a brief time period.

Powles and Barans (1980) estimated density of *C. striata* in the sponge-coral habitat of the South Atlantic Bight. The estimates of 51 fish/ha and 7.6 kg/ha derived from the data of Powles and Barans (1980) were 37-66% and 23-44% of our mark-recapture values. Powles and Barans (1980) indicated that possible sources of error in their study were distance determinations from loran-A, which are much less precise than distances derived from loran-C readings, and variable visibility.

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NOTES

COMPARISON OF VISCERAL FAT AND GONADAL FAT VOLUMES OF YELLOWTAIL ROCKFISH, *SEBASTES FLAVIDUS*, DURING A NORMAL YEAR AND A YEAR OF EL NIÑO CONDITIONS

One of the severest El Niño events of the century occurred off California during late 1982 and most of 1983 (Rasmusson 1984). Associated with the warm water and lack of upwelling were impressions by many fishermen and biologists that macroplanktonic organisms were at low densities and that fish were thinner than normal. A semiquantitative sampling program off of San Francisco indicated that euphausiids, a major component of the macroplankton, were considerably less common in 1983 than in either 1982 or 1984 (Smith[1]).

Yellowtail rockfish are abundant off northern California and are an important component of recreational and commercial catches in some areas. The species feeds mostly on macroplanktonic organisms such as euphausiids, salps, and small fish (Phillips 1964; Pereyra et al. 1969; Lorz et al. 1983). Annual cycles of visceral fat volume and gonad volume are documented in Guillemot (1982) and Guillemot et al. (1985). The studies showed that visceral fat volume in both sexes of yellowtail rockfish is at a maximum during fall. The viviparous species (Boehlert and Yoklavich 1984) mates in early fall (September) and releases larvae during winter (January-March) (Wyllie Echeverria[2]). Guillemot (1982) and Guillemot et al. (1985) showed that male gonad volumes peak in fall and female gonad volumes peak in winter.

The purpose of this study is to determine possible effects of El Niño conditions by comparing visceral fat and gonad volumes during 1983, a year of El Niño conditions, with data collected during 1980, a normal year (Guillemot 1982).

Methods and Materials

Guillemot (1982) and Guillemot et al. (1985) utilized data collected throughout the year. The 1983 data were collected only on 21 September, the approximate sexual activity peak for males, and 20 December, which slightly precedes the peak time of larval release for females. Only 1980 data collected within 20 d of the two 1983 collection dates and samples collected from central California, between Bodega Bay and Half Moon Bay, were used in this study. In 1983 all specimens were collected from landings made at Bodega Bay.

Specimens were sexed, measured to the nearest millimeter for total length, and viscera were removed and preserved in 10% buffered Formalin[3] in the field following the procedures of Guillemot et al. (1985). After about 90 d of storage, visceral fat and gonad volumes were measured to the nearest milliliter by water displacement. Visceral fat of some fish had dissolved to form a floating liquid. The volume of this liquid was measured and added to the total fat volume. Data from males larger than 379 mm, when 90% are mature, and from females larger than 380 mm, when 85% are mature, were used (Wyllie Echeverria fn. 2).

As in Guillemot (1982) and Guillemot et al. (1985) we used the following power equation to describe the relationship between fat or gonad volume and length:

$$Y = \alpha X^{\beta}$$

where Y = fat or gonad volume, and
X = total length.

The parameters were estimated by first transforming the variables to natural logarithms and then using standard least squares linear regression techniques. Analysis of covariance was used to determine if separate lines for the two years significantly reduced the variance from a common line (Kleinbaum and Kupper 1978). This is a fairly robust test in that if there is not a significant linear relationship between the two variables for one or both time periods, the test is nearly as powerful for comparing the two means as an analysis of variance.

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[1] Smith, S. Unpublished data. Tiburon Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[2] Wyllie Echeverria, T. 1983. Reproductive seasonality and maturity of the rockfishes (Scorpaenidae; *Sebastes*) off central California. Unpubl. manuscr., 66 p. Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

The regression lines for the male fat volume for the two years intersect and are not significantly different (Table 1). The results of the analysis of covariance for fat volume of females are highly significant (Table 1). Females had significantly higher fat volumes in 1980 for both months (Fig. 1).

The comparisons of gonad volumes produced highly significant results in December for both sexes, and for females in September (Table 2). Female gonad volumes were higher in 1980 during December and lines intersected in September (Fig. 2). Male gonad volumes were significantly higher in December 1983 than in December 1980.

The seasonality of gonad development was similar in the two years, but appeared to be delayed in 1983.

TABLE 1.—Results of analysis of covariance of fat volumes of yellowtail rockfish regressed on length. Observations were transformed to natural logarithms for the analysis.

		1980			1983			
Sex	Month	Sample size	Intercept	Slope	Sample size	Intercept	Slope	*F*
Male	September	20	−9.884	2.011	38	22.272	−3.355	2.753
Male	December	17	7.198	−0.978	35	35.402	−5.693	2.571
Female	September	25	−9.327	2.003	46	5.443	−0.449	11.917**
Female	December	19	21.813	−3.262	50	1.609	−0.058	5.889**

**Significant at 99% level of confidence.

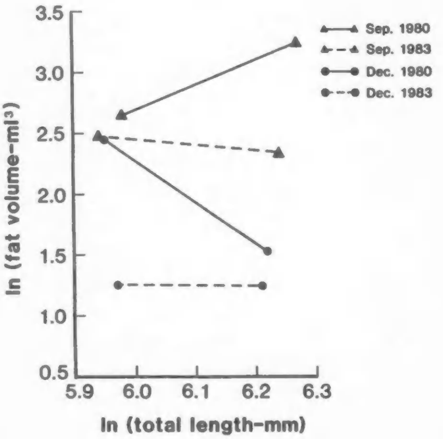

FIGURE 1.—Relationships between ln (visceral fat volume) and ln (total length) for female yellowtail rockfish in 1980 and 1983.

Males were 50% maturing and 50% resting in September 1980, and 100% resting during December. In 1983 males were 100% maturing during September, and 8% maturing and 92% resting during December. Females were 35% maturing and 65% resting in September 1980, and 83% maturing and 17% resting in December. In 1983 females were 100% maturing during September, and 97% maturing and 2% resting during December. Data on season or parturition for 1981-84 (Table 3) indicate that parturition was delayed in 1983 and 1984 compared with 1981 and 1982.

Discussion

The results tend to agree with expectations. Female fat volumes were lower in 1983 than in 1980, which is in agreement with the impressions of fishermen and the expectation that El Niño would produce relatively poor feeding conditions and consequently result in thin fish.

TABLE 2.—Results of analysis of covariance of gonad volumes of yellowtail rockfish regressed on length. Observations were transformed to natural logarithms for the analysis.

		1980			1983			
Sex	Month	Sample size	Intercept	Slope	Sample size	Intercept	Slope	*F*
Male	September	20	−35.589	6.161	38	−25.205	4.450	0.274
Male	December	17	−50.003	8.290	35	−11.037	1.962	8.170**
Female	September	25	−54.09	9.171	46	−31.019	5.406	3.404*
Female	December	19	−56.674	9.855	50	−45.723	7.908	12.224**

**Significant at 99% level of confidence.
*Significant at 95% level of confidence.

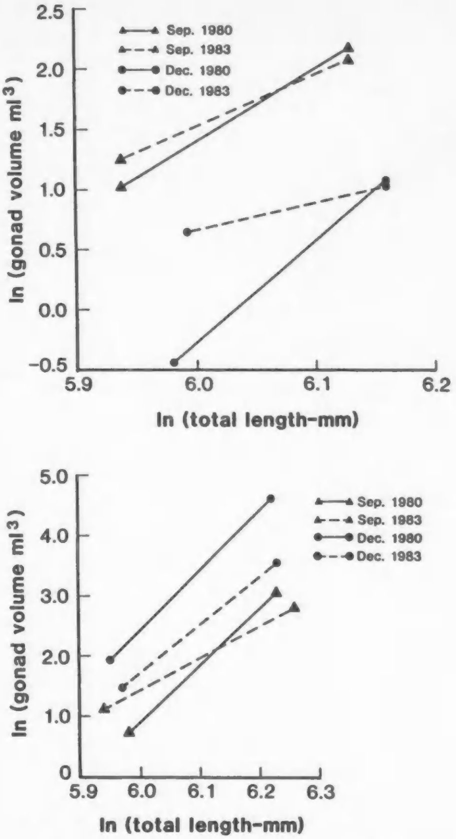

FIGURE 2.—Relationships between ln (gonad volume) and ln (total length) for yellowtail rockfish in 1980 and 1983. (Top) males; (bottom) females.

TABLE 3.—Percent of yellowtail rockfish females with eyed-larvae observed in samples collected in central and northern California, 1981-1984.

Year	January	February	March	April	May	June
1981	5	0	0	0	0	0
1982	0	15	0	0	0	0
1983	0	18	16	6	0	4
1984	3	10	15	0	0	0

The lower ovary volumes in 1983 than 1980 could have been related to either delayed parturition and/or lower reproductive effort. Wootton (1979) described relationships between feeding conditions and fish fecundity. The significantly higher gonad volumes for males in December 1983 compared with 1980 were not expected. December is later than the normal period of sexual activity for males, but the unexpected gonad volume results may be caused by delayed mating. The gonad stage data indicated that male sexual activity was later in 1983 than in 1980.

While fish condition and reproduction were different in 1983 than in the preceding non-El Niño years, the documentation of such differences for marine fish is uncommon. The season of parturition of yellowtail rockfish is more variable than we realized when the study was designed and the data on fish condition and gonad volume should have been collected over a wider period of time. The results of our study indicate that the assumption of constant adult fish condition and reproductive effort that is usually made in models of the population dynamics of fish is questionable.

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WILLIAM H. LENARZ
TINA WYLLIE ECHEVERRIA

Southwest Fisheries Center Tiburon Laboratory
National Marine Fisheries Service, NOAA
3150 Paradise Drive
Tiburon, CA 94920

DIEL FORAGING ACTIVITY OF AMERICAN EELS, *ANGUILLA ROSTRATA* (LESUEUR), IN A RHODE ISLAND ESTUARY

Although the American eel, *Anguilla rostrata* (LeSueur), is abundant and commercially exploited along the entire Atlantic coast of North America, its basic biology is not well understood (Tesch 1977; Fahay 1978; Helfman et al. 1984). Foraging activity has not been studied. Helfman et al. (1983) examined daily movement patterns in an estuary and found, as had laboratory studies (Bohun and Winn 1966; Edel 1976; van Veen et al. 1976; Westin and Nyman 1979), that American eel locomotor activity is nocturnal and suggested that American eel foraging activity is also nocturnal. This study sought to describe the diel foraging patterns of wild estuarine American eels by monitoring capture rates in baited eel traps on a 24-h basis.

Eight eel traps were set 10 m apart along a transect in a tidal portion of the Pettaquamscutt River estuary, R.I. The water was turbid (the bottom could not be seen at midday in areas <1 m deep) and the salinity ranged from 20 to 30‰, depending on the tide. Cylindrical traps are commercially constructed of 0.64 cm^2 wire mesh and are 78 cm long and 20 cm in diameter with two single funnel openings of 5 cm in diameter. The traps were baited with 500-700 g pieces of freshly killed horseshoe crab, *Limulus polyphemus*, an effective eel bait (Bianchini et al. 1981).

Capture rates probably reflected contemporaneous foraging because the traps were thought to have a high escape rate. A high escape rate was suspected for two reasons: 1) When we changed from checking the traps once every afternoon to once every 3 h, the daily capture rate increased nearly 50 fold; and 2) when 40 eels were placed into 4 unbaited traps in the river, only 1 eel remained 24 h later. Feeding activity in the traps was evidenced by several factors: an examination of the gut content of 10 captured eels found 6 to contain horseshoe crab and the rest to be empty, anesthetized animals frequently regurgitated bait, eels were often found burrowing in the bait, and unbaited traps rarely caught anything.

Starting at 1200 e.d.t., traps were checked and rebaited at 3-h intervals for six 24-h periods evenly spaced over a 15-d span in early September 1982. This design removed any possible tidal influence because the lunar tidal period is 14.8 d. Within 10 min of their capture, eels were released 10 m to one side of the transect's center point. Traps were rebaited every 6 h or whenever the bait was found to have been consumed (which rarely occurred). Baiting schedules were designed so that every other trap was rebaited at each 3-h check, and all portions of the crabs (heads and tails of both males and females) were equally distributed with respect to time and location. A total of 322 American eels were captured (some were probably recaptures): 178 (55% of the total) were caught just after sunset at 2000 e.d.t., 140 (44%) were caught during the remainder of the night, and 4 (1%) were caught during daylight (Fig. 1). Although daily capture rates were variable and ranged from 113 to 22, all exhibited this pattern.

To determine when foraging activity commenced, the traps were checked and rebaited at 30-min intervals between 1715 e.d.t. (40 min before sunset) and 2015 e.d.t. for 6 evenings during a 15-d period in early October. Eels were consistently first captured just after sunset, with captures peaking 1 h after sunset and declining thereafter (Fig. 2). Daily capture totals varied considerably but all exhibited this

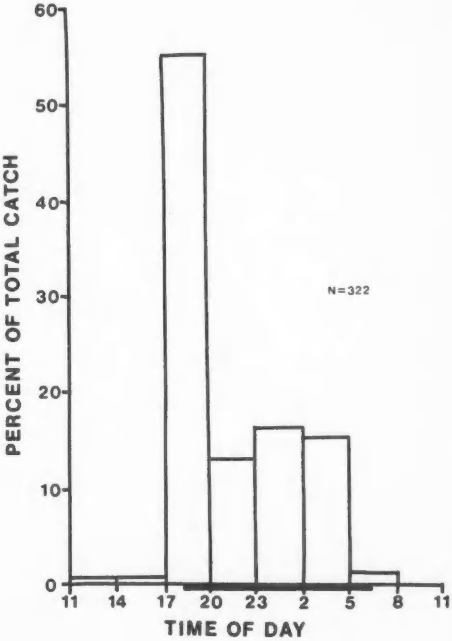

FIGURE 1.—Percentage of total catch of American eels by time of day for the 24-h experiment. The histograms cover the time between checks; i.e., their right boundaries mark the times when traps were checked. The bold section of the x-axis denotes the period between sunset and sunrise.

pattern. A total of 588 American eels were captured, 83% more than in the 24-h experiment, possibly reflecting the intensity of foraging activity just after sunset. To characterize the population, eels caught on the third evening were measured. They had an average total length of 30.7 cm (SD = 5.4, n = 121), and 10 of the 121 animals caught had the silvered pigmentation pattern which characterizes maturing individuals (Tesch 1977).

These data show that the foraging activity of estuarine American eels in late summer through autumn is nocturnal and peaks sharply at nightfall. Whether the subsequent decline in captures was caused by a decrease in foraging because of satiation or by an unrelated decline in locomotor activity cannot be determined. The swimming activity of unfed eels in the laboratory often exhibits a dramatic peak at lights-off (Bohun and Winn 1966; Edel 1976; van Veen et al. 1976). Spring and autumn captures of wild short-finned New Zealand eels, *Anguilla australis schmidtii*, in baited traps displayed the nocturnal activity pattern described here (Ryan 1984). However, capture patterns in the latter study changed with the season, as did the locomotor patterns of the yellow European eel, *Anguilla anguilla*, studied by Westin and Nyman (1979). Further research is required to understand the relationship between foraging and locomotor activity patterns and how environmental and physiological factors might influence them.

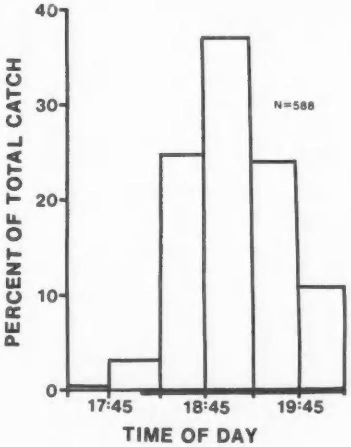

FIGURE 2.—Percentage of total catch of American eels by time of day for the evening experiment. The histograms cover the time between checks; i.e., right boundaries mark the times when traps were checked. The bold section of the x-axis denotes the period after sunset.

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PETER W. SORENSEN

Graduate School of Oceanography
University of Rhode Island
Narragansett, RI 02882
Present address:
Zoology Department
University of Alberta
Edmonton, Alberta T6G 2E9, Canada

MARCO L. BIANCHINI

Graduate School of Oceanography
University of Rhode Island
Narragansett, RI 02882
Present address:
I.P.R.A., Consiglio Nazionale Delle Ricerche
Via Nizza 128
00188 Roma, Italy

HOWARD E. WINN

Graduate School of Oceanography
University of Rhode Island
Narragansett, RI 02882

FIRST RECORD OF THE LONGFIN MAKO, *ISURUS PAUCUS*, IN THE GULF OF MEXICO

The longfin mako, *Isurus paucus*, (Guitart-Manday 1966) is a large, pelagic shark that has been reported from the western Indian, central Pacific, eastern North Atlantic, and the western North Atlantic Oceans (Compagno 1984). Guitart-Manday (1975, cited by Dodrill and Gilmore 1979) described the longfin mako as a relatively common catch of pelagic longliners off northwest Cuba. They are usually captured off the continental shelf at depths of 60-120 fathoms and infrequently at 10-50 fathoms. Dodrill and Gilmore (1979) reported the first North American continental longfin mako, found beached in the surf at Melbourne Beach, FL. This paper reports the first recorded occurrence of the longfin mako in the Gulf of Mexico.

A large female *I. paucus* was collected 1 April 1985 by longline fisherman, 80 mi south of Panama City, FL (lat. 28°55′N, long. 85°35′W) near the surface, over 300 fathoms of water. Standard length (precaudal length) measured 313.0 cm and fork length measured 342.0 cm. Total length could not be measured directly because of the sharks position on the boat deck and was estimated using a ratio of total length to fork length (TL/FL = 1.152) calculated from 7 large *I. paucus* (Harold Pratt[1]). Using this ratio, total length was estimated to be ca. 390 cm. Although no embryos were present in the oviduct, this fish appeared reproductively mature. The oviducts were 3-4 cm in diameter and ovarian eggs measured 2-3 mm in diameter. Gilmore (1983) proposed the reproductive strategy of *I. paucus* to be oviphagous, as remnants of yolk were found in the digestive tract and mouth of an examined embryo.

The ventral surface of the snout and gill areas of our shark exhibited a dark grey coloration. Garrick (1967) reported this coloration as an important distinguishing characteristic between *I. paucus* and the shortfin mako, *I. oxyrinchus*, which exhibits a creamy white coloration in that area. Gilmore (1983) reported the dusky coloration to be more extensive in larger *I. paucus*.

Pectoral fin length of our shark measured 80.6 cm. Gilmore (1983) compared an adult and embryo *I. paucus* and found that the pectoral fin length represented a greater percentage of SL in the embryo (31% of SL) than in the adult (28% of SL). Our Gulf of Mexico specimen was slightly larger than the specimen reported by Gilmore (1983) (313.0 cm vs 303.5 cm SL), and the pectoral fin represented 26% of SL. Guitart-Manday (1966) examined smaller *I. paucus*—195, 203, and 226 cm TL—and found pectoral fin length as percent total length to be 30.4%, 30.0%, and 29.2%, respectively. For this specimen, pectoral fin length as percent TL was about 21%. It appears that as *I. paucus* increase in length, the pectoral fins do not increase proportionately, resulting in reduced pectoral length to total length ratios in larger sharks.

This record suggests that the longfin mako at least occurs infrequently in the northern Gulf of Mexico. Three male *I. paucus* (191, 193, and 220 cm SL) captured 16 April 1985 off the Mississippi River (lat. 27°35′N, long. 89°55′W) further supports this suggestion (Stephen Branstetter[2]). These captures extend the known range of this species well into the northern Gulf of Mexico.

Acknowledgments

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[2] Stephen Branstetter, Department of Wildlife and Fisheries Science, Texas A&M University, College Station, TX 77843-2258, pers. commun. August 1985.

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Kristie Killam
Glenn Parsons

Department of Marine Science
University of South Florida at St. Petersburg
140 7th Avenue South
St. Petersburg, FL 33701

MOVEMENT OF SEA-RUN SEA LAMPREYS, *PETROMYZON MARINUS*, DURING THE SPAWNING MIGRATION IN THE CONNECTICUT RIVER[1]

Adult sea lampreys, *Petromyzon marinus*, first enter New England rivers in late March and early April (Bigelow and Schroeder 1953). The only information on river water temperatures during the migration were collected in 1974 from the St. John River, New Brunswick, where Beamish and Potter (1975) captured the first prespawning adults in a fish lift at Mactaquac Dam (river km 140) at 13°C in mid-June and the run peaked at 17°-19°C. Because thousands of sea lampreys are annually passed upstream of Holyoke Dam (river km 140) on the Connecticut River, the passage records provide an ideal opportunity to characterize the run relative to temperature. River flow was partially or totally controlled by the hydroelectric facilities at the dam, so we did not examine the effects of flow on the run.

The behavior and rate of movement of landlocked sea lampreys in the Great Lakes was determined using mark and recapture of adults at stream weirs (Applegate 1950; Applegate and Smith 1950; Smith and Elliot 1952; Moore et al. 1974). The only estimate of the rate of movement of sea-run sea lampreys was done by Beamish (1979) who used the energy expended during an upstream movement to estimate the distance traveled and the rate of movement of adults in the St. John River. Because this estimate of the rate of movement was not verified by direct observations on fish in the field, we believed that additional study was necessary. We selected radio telemetry to determine the rate of movement and diel behavior of sea lampreys. The abundance, size, and sex ratio of the Connecticut River population were reported by Stier and Kynard (1986).

Methods

Radio-tagged sea lampreys were observed in the 46 km stretch of the Connecticut River from Brunelle's Marina to Cabot Station, a hydroelectric facility located 4.5 km below Turners Falls Dam (Fig. 1). The downstream half of this stretch flows slowly, creating a deep channel and shoals; the upstream half flows swiftly with pools and riffles. Major spawning areas are in the upper main-stem near Cabot Station, Russelville Brook, and the Fort, Mill, Sawmill, and Deerfield Rivers (Fig. 1).

The number of sea lampreys passed daily by the fish lifts from 1980 to 1983 were counted by personnel of the Massachusetts Cooperative Fishery Research Unit. Daily maximum river temperature was recorded at Holyoke Dam.

Sea lampreys were captured in the trap at the fish lifts during May and June 1982, measured for total length, and held for <24 h in a 1,325 L circular tank supplied with river water. We anesthetized fish with MS-222 (1:20,000) and tagged them first with a Floy tag inserted through the posterior dorsal fin, and second with a transmitter placed on the left side of the body along the first dorsal fin. Sex could not be accurately determined visually.

Cylindrical radio transmitters were constructed from the design of Knight (1975) and operated at a frequency of 30.05-30.25 MHz. Tags measured 34 × 10 mm, weighed 3.5-4.5 g in air, and transmitted for about 20 d. Each fish was identified by frequency and pulse rate. We located fish to within about 10 m, using receivers equipped with an omnidirectional, 1/8-wave antenna and a directional, tuned-loop antenna.

We released two to six sea lampreys at a time and observed them continuously for ≥6 h or until darkness. Subsequently, sea lampreys were located each day until they reached Cabot Station or entered a tributary. During all surveys, we noted the locations of fish to the nearest river kilometer. Diel movement was monitored for five 24-h periods. Additional fish were released during the day for this study.

Results and Discussion

The water temperatures, and the year in parentheses, when sea lampreys first entered the fish lifts were 12.5°C (1980), 10.5°C (1981), 12.5°C (1982), and 15.5°C (1983) (Fig. 2). The lifts sampled the en-

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[1] Contribution No. 101 of the Massachusetts Cooperative Fishery Research Unit, which is supported by the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries, and the University of Massachusetts.

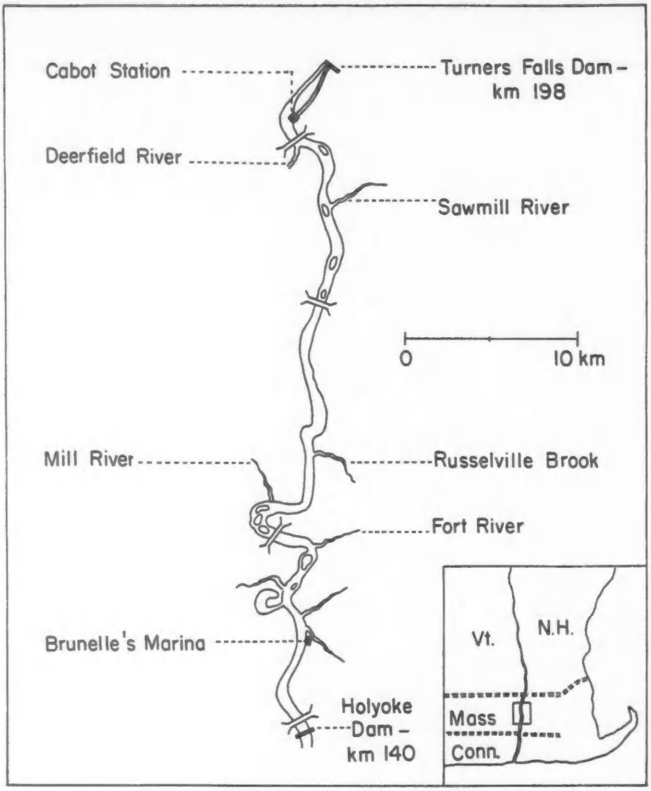

FIGURE 1.—Section of the Connecticut River from river km 140 to 198, showing the locations of the Holyoke and Turners Falls Dams, the release site for radio-tagged sea lampreys at Brunelle's Marina, and the major spawning tributaries between the two dams.

tire run each year except in 1981 when sea lampreys were present in the first lifts of the year (the lifts began operating on 29 or 30 April of each year). During the peak 7 d, the temperature ranges, and year in parentheses, were 16°-19°C (1980), 17°-19°C (1981), 16°-17°C (1982), and 17°-21°C (1983). Movement into the fish lift ceased at 24°C in 1983 and at 21°-22°C in the other years (Fig. 2).

Information on the maximum daily temperature during the migration of landlocked sea lampreys in a large river comes from the Ocqueoc River (Lake Huron drainage) which for some years supported an annual run of 25,000-40,000 (Applegate 1950; Applegate and Smith 1950). The temperatures, and date in parentheses, when the first sea lampreys entered a weir near the mouth of the river were 10°C (27 April 1949) and 6°C (11 May 1950); and the run peaked at 14°-17°C (first week of May 1949) and 18°-20°C (third week of May 1950). Most movement at the weir ceased at 21°C (about 11 July), but during both years one or two sea lampreys per day continued to enter the weir throughout the summer at 22°-26°C.

The temperature regimes in the Ocqueoc and Connecticut Rivers during the peak and at the end of the principal migration were in general agreement. Runs peaked at 14°-20°C in the Ocqueoc River and 16°-21°C in the Connecticut River; most of the run ceased at 21°C in the Ocqueoc River and at 21°-24°C in the Connecticut River. The migrations differed because a few adults in the Ocqueoc River continued to migrate throughout the summer, whereas none were captured after 25 June during 3 yr in the Connecticut River. Therefore, even

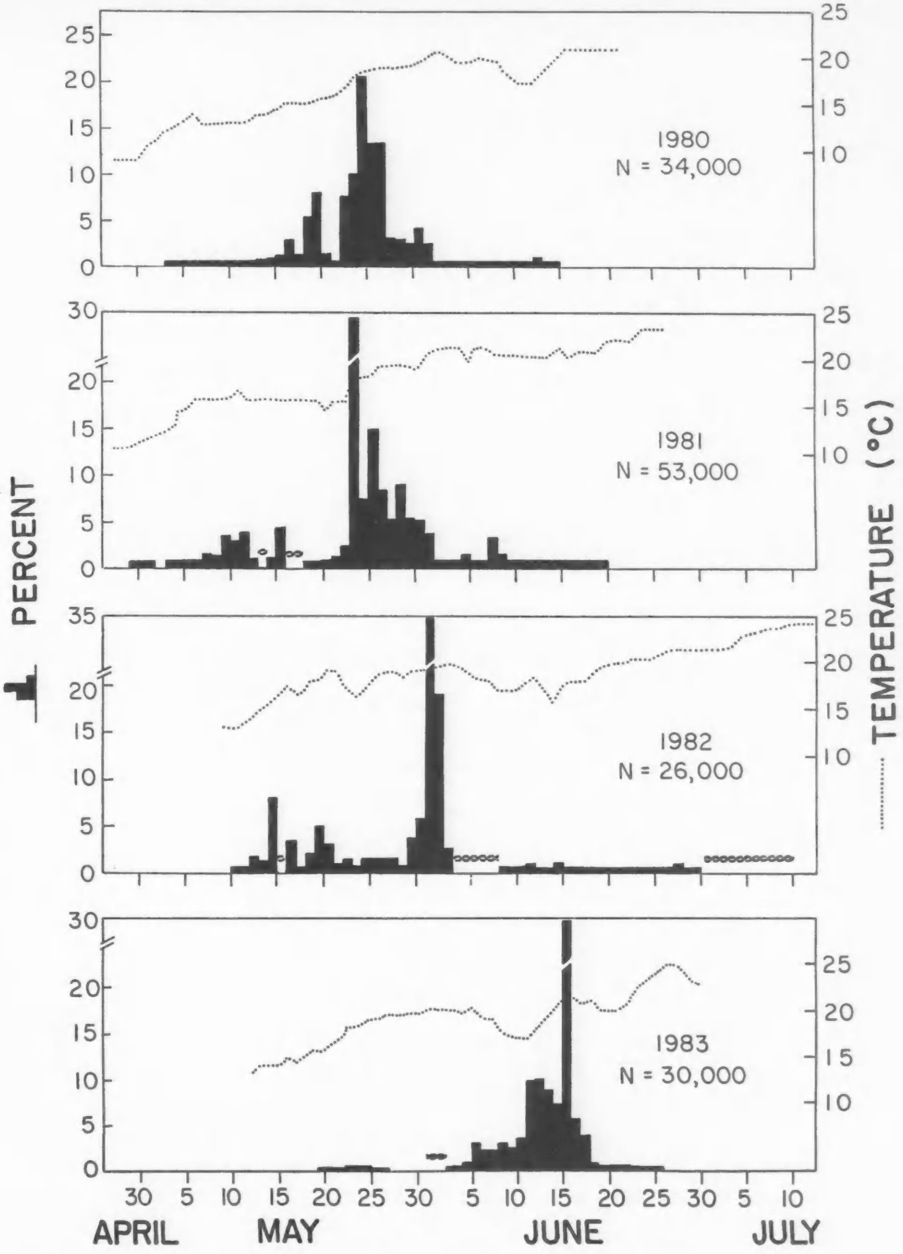

FIGURE 2.—Daily percent of total sea lampreys lifted at the Holyoke fish lifts each year, 1980-83. Temperatures are the daily maximum river temperatures. The lifts began operating about 1 May in all years and ceased about 15 July. Wavy line near the base of each panel identifies days on which the lifts were not operated.

though the data from the two runs differed greatly in time and space, the general migration pattern in relation to river temperature was remarkably similar.

The behavior of the sea lampreys in the St. Johns and Connecticut Rivers also appeared similar. In 1974, the first migrants were collected at 13°C at the Mactaquac fish lift (Beamish and Potter 1975), and from 1980 to 1983 the first migrants were passed in the Holyoke fish lift at 10.5°-15.5°C. The peak of the run was also similar—17°-19°C in the St. Johns River and 16°-21°C in the Connecticut River.

Mean length of the 45 sea lampreys tagged was 73.2 cm (range, 63.0-80.0 cm). Five were not relocated either because the tag failed or the fish moved downstream over the dam. No tagged sea lamprey died during the study. The remaining 40 fish were followed for a total of 224 h during 24 d (12 May-4 June; Fig. 3). Since sea lampreys migrated upstream at Holyoke until 30 June 1982 (Fig. 2), for the most part we observed the movement of early migrants. During the study, water temperature increased from 13° to 22°C; river discharge gradually decreased from 60.4 m^3/s on 12 May to 50.9 m^3/s on 31 May. Twenty sea lampreys moved >23 km and 4 reached Cabot Station. Nineteen were last located near the mouths of the Fort or Mill Rivers or Russelville Brook (Fig. 1). Spawning of tagged fish was verified in the tributaries—an indication that normal behavior resumed after the sea lampreys were tagged.

Sea lampreys moved upstream at ground speeds of 0.1-3.5 km/h. The daily mean rate of movement including rest periods was 1.01 km/h ± 0.75 (mean ±SD; range, 0.1-2.7 km/h; N = 40) or 0.4 body length/s. The mean rate, excluding rest periods, was 1.51 km/h ± 0.53 (range, 0.1-3.5 km/h; N = 39) or 0.6 body length/s. Early migrants moved a mean of 0.1-1.2 km/h; and three migrants that were observed during the peak passage at the fish lift on 2 June had the fastest mean daily rate of 2 km/h (Fig. 3).

Among landlocked sea lampreys, early migrants have a slower rate of movement than peak migrants because they rest more (Applegate 1950; Skidmore 1959; Larsen 1980). Our observations during the peak period after 30 June did not indicate a sustained increase in the rate of movement (Fig. 3). Because we only observed a few peak migrants, additional study is necessary to compare the rates of movement between early and peak migrants.

The movement rates of sea lampreys in the Connecticut River were the highest reported for the species. Landlocked sea lampreys moved at much lower rates of 0.02-0.21 km/h (Applegate and Smith 1950; Skidmore 1959; Wigley 1959). Beamish (1974) found a maximum swimming speed of 1.08 km/h (30 cm/s) for landlocked adults in the laboratory. Using the energetics of adult sea-run sea lampreys during a 35-d upstream move into the fish lift at Mactaquac Dam on the St. John River, Beamish (1979) estimated the rate to be 0.23 km/h for males and 0.26 km/h for females, or 0.1 body length/s for both. This rate was similar to that of the landlocked form. Because the sea-run adults are much larger than landlocked adults, they should swim faster. Our results suggest that the 0.2 km/h rate which was estimated for the St. John River adults may be incorrect, possibly because the fish were delayed

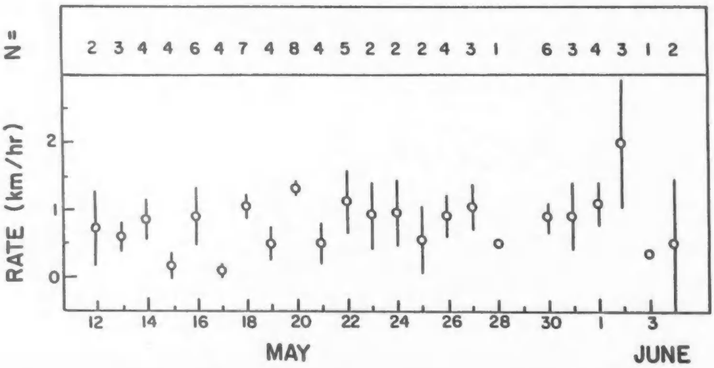

FIGURE 3.—Daily mean rates of movement of radio-tagged sea lampreys (open circles). (Vertical lines show standard errors; numbers of lampreys monitored are shown above each mean.)

several days before finding the entrance to the fish lift at Mactaquac Dam.

Diel movement rates were monitored on 13 and 17 May (early migrants) and 26 and 30 May and 1 June (peak migrants). Movement was slowest from 1200 to 1700 h (Fig. 4). Nocturnal behavior was strongest among the early migrants; peak migrants had a higher rate of movement because they also moved during the day (mornings only). A similar pattern for landlocked adults was found by Kleerekoper et al. (1961).

In summary, except for the longer summer migration and the slower rate of upstream movement, the behavior of sea-run sea lampreys in the Connecticut and St. Johns Rivers was similar to that of the landlocked sea lampreys in the Ocqueoc River. The timing of the runs in relation to temperature and the diel movement patterns appears very stable, probably with important survival or reproductive advantages.

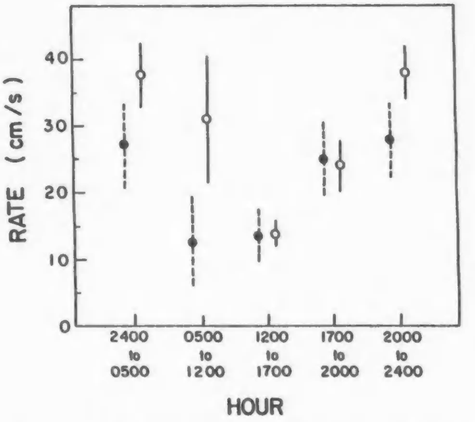

FIGURE 4.—Mean movement rates of early migrants (solid circles) monitored 13 and 17 May (N = 13), and peak migrants (open circles) monitored 26 and 30 May and 1 June 1982 (N = 7). (Vertical lines show standard errors.)

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KATHLEEN STIER
BOYD KYNARD

Massachusetts Cooperative Fishery Research Unit
University of Massachusetts
204 Holdsworth Hall
Amherst, MA 01003

VARIATIONS IN THE MORPHOLOGY OF *FISTULICOLA PLICATUS* RUDOLPHI (1802) (CESTODA:PSEUDOPHYLLIDEA) FROM THE SWORDFISH, *XIPHIAS GLADIUS* L., IN THE NORTHWEST ATLANTIC OCEAN

During the course of a survey of the helminth parasites of the swordfish, *Xiphias glasius* L., from the Northwest Atlantic Ocean, several morphological variations were observed in specimens of the pseudophyllidean tapeworm, *Fistulicola plicatus*. The most notable of these variations were pseudoscolex form and proglottid shape and size. Methods of scolex attachment to the organ wall, descriptions of pseudoscolex structures, and organ specific variations in the morphology of *F. plicatus* are given.

Materials and Methods

A sample of 303 gills and gastrointestinal tracts of swordfish was collected from four geographical areas in the Northwest Atlantic Ocean in the late summer and early fall of 1980. The areas sampled and the number of swordfish collected from each geographical area are as follows: Cape Hatteras (74), Georges Bank (90), Scotian Shelf (69), and Grand Bank (70); all collected by longline gear and frozen at sea. The swordfish were later dissected and examined for helminth parasites in the laboratory.

Pseudophyllidean cestodes were removed from the infected organ and fixed whole in 70% alcohol or 10% Formalin[1]. Several infected organs were fixed whole in Bouin's fluid or 10% Formalin. Specimens used for taxonomic examinations were stained in Erlich's hematoxylin, Blachin's lactic acid carmine, or Semichon's aceto-carmine. Camera lucida drawings were made from fixed, unstained specimens.

Results

Fistulicola plicatus has been reported from the swordfish by Linton (1901), Cooper (1918), Nigrelli (1938), and Iles (1970). In this study *F. plicatus* was found in the intestines and rectums of swordfish from all four sampling areas. Considerable morphological variation was found between individuals of this species. Variations were in scolex form, overall parasite length, and proglottid shape and size. About 50% of specimens recovered exhibited a scolex and proglottid structure characteristic of specimens described by Yamaguti (1959). Scolices from these were arrow-shaped and possessed two simple, leaf-shaped bothridia (Fig. 1). Any variation from this scolex form were considered to be pseudoscolices. Proglottids from specimens described by Yamaguti (1959) were short and broad with foliate lateral edges. Internal proglottid morphology was not easily seen in any of the specimens examined during the present study, although nerve trunk location (near lateral margins), cirrus-sac and vagina location (on opposite lateral margins), and egg shell structure (thick-shelled and operculate) were occasionally observable.

A total of 29 specimens recovered had penetrated the wall of the infected organ. Occasionally the tapeworms penetrated the organ wall and retained typical scolex form, i.e., arrow-shaped with simple, well-developed bothridia but, in the majority of cases, complete perforation of the organ wall resulted in the formation of a pseudoscolex. Attachment to the organ wall (rectum and intestine) was achieved in the following four ways:

1) By complete perforation of the organ wall, the scolex and a portion of the neck encapsulated in a rounded, host-produced cyst attached to the organ serosa. Scolices recovered from these cysts were usually arrow-shaped with typical bothridia, or occasionally found as a round, transparent, fluid-filled bag, which possessed rudimentary or no apparent bothridia (Fig. 2).
2) By complete perforation of the organ wall, the scolex and a portion of the neck encased in a tubular, host-produced sheath, attached along its entire length to the organ serosa. Occasionally this sheath was entwined with the mesenteries associated with the infected organ. Pseudoscolices found within these sheaths were long, rounded, and slender, and exhibited no bothridia (Fig. 3).
3) By complete penetration of the organ wall, the scolex markedly enlarged (up to 6 cm in length), lying free, and unencapsulated in the peritoneal cavity. Pseudoscolices of this type were long, broad, pseudosegmented, and possessed well-developed bothridia (Fig. 4).
4) In this case the scolex did not fully penetrate the organ wall, but perforated the wall to a slight depth, and remained in that position. Often specimens were found to exhibit this slight organ wall penetration and re-emerge into the lumen of the organ. In these cases the

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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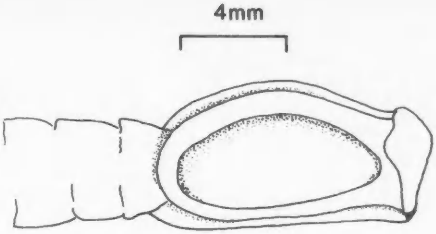

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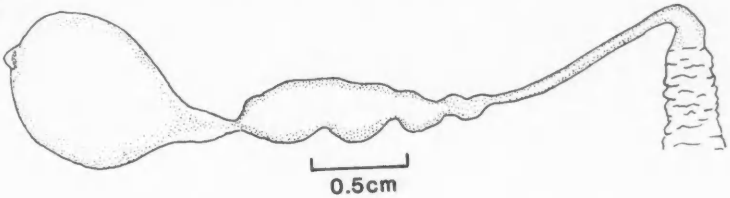

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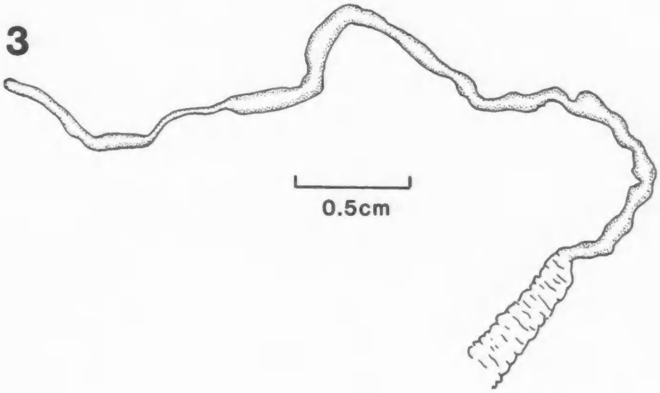

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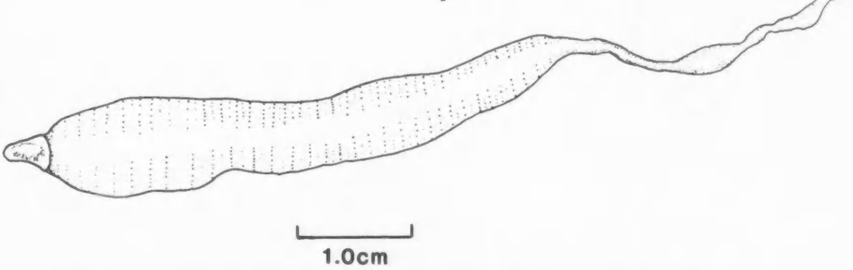

Figure 1.—Typical scolex from *Fistulicola plicatus*, as described and figured by Yamaguti (1959).

Figure 2.—Pseudoscolex (1st type).

Figure 3.—Pseudoscolex (2d type).

Figure 4.—Pseudoscolex (3d type).

1) scolex type described by Yamaguti (1959) was retained.

Fistulicola plicatus specimens recovered from the lumen of the intestines were morphologically different from those collected from the rectum. They were long, up to 1 m in length, and exhibited longer, less-broad strobila than those characteristic of the rectal forms. All specimens of *F. plicatus* recovered from the anterior portion of the intestine exhibited the previously described first type of scolex attachment to the organ wall, i.e., the scolex perforated the organ wall and was encapsulated in a rounded, host-produced cyst attached to the intestinal serosa. The scolex penetrated the anterior portion of the intestine, with the strobila projecting posterior through the length of the organ. Very small *F. plicatus* were found in the posterior portion of the intestine. These exhibited shallow penetration by an unmodified scolex.

Fistulicola plicatus specimens found in the rectum of swordfish were usually <20 cm in length and possessed very broad strobila. These rectal forms exhibited all of the previously described types of scolex attachment and structure, penetrating the organ wall near the rectal sphincter (Fig. 5). Occasionally, several tapeworms were found with their necks passing through a single perforation of the rectal wall, their scolices jointly encapsulated in a rounded serosal cyst.

Discussion

Apex type predators such as the swordfish eat and digest large amounts of prey species and, consequently, the intestines and rectums of these fish exhibit high levels of muscular activity. Without perforation of the organ wall (by the scolex and neck), many tapeworms would probably be voided with the faeces. The development of the pseudoscolex is an adaptation for anchoring the simple, unarmed scolex to the organ wall. It is clear that *F. plicatus* secretes a powerful digestive enzyme which enables the scolex to penetrate the very muscular walls of the intestine and rectum of swordfish. Iles (1970) found many examples of pseudoscolex variation in 24 specimens from swordfish in the Northwest Atlantic Ocean. Several of these variations are similar to those found in this study. It is obvious from this study, and studies such as Iles (1970), that *F. plicatus* is a very adaptable tapeworm and will develop any pseudoscolex structure which is neces-

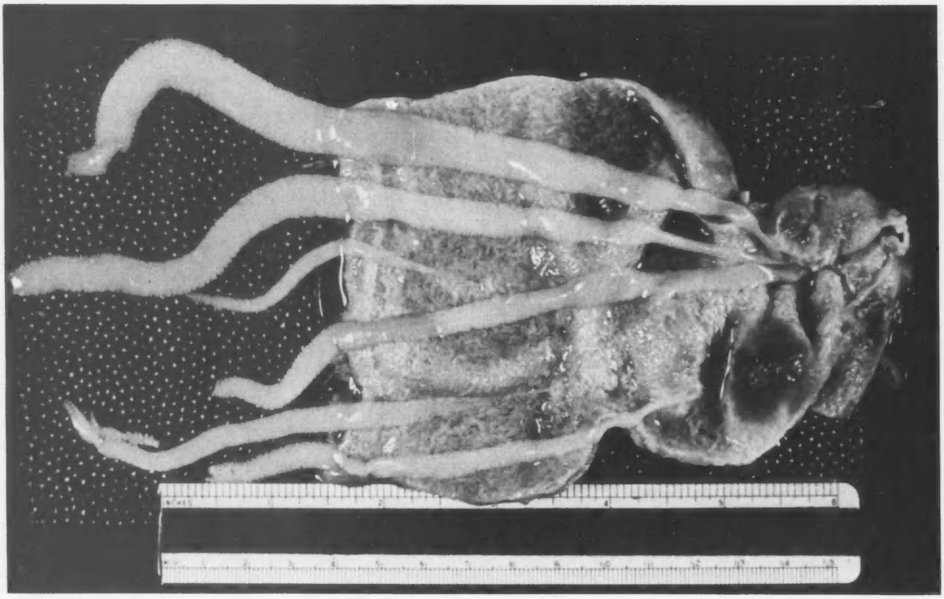

FIGURE 5.—*Fistulicola plicatus* (in situ) from rectum of *Xiphias gladius*.

sary to anchor itself to the organ wall. Large samples of swordfish intestines and rectums will invariably show many variations in the pseudoscolex structure of *F. plicatus*.

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W. E. HOGANS

Identification Centre
Department of Fisheries and Oceans
Biological Station
St. Andrews, Nova Scotia E0G 2X0, Canada

P. C. F. HURLEY

Marine Fish Division
Bedford Institute of Oceanograph
Department of Fisheries and Oceans
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2, Canada

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